THE PHYSICAL AND

ECONOMIC FOUNDATION OF NATURAL RESOURCES

I

Photosynthesis

Basic Features of the Process

INTERIOR AND INSULAR AFFAIRS COMMITTEE

HOUSE OF REPRESENTATIVES, UNITED STATES CONGRESS

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DOCUMENTS EXPEDITING PROJECT

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Foreword

THIS IS THE FIRST in a series of publications designed to present the results of new and productive research on the basic physical and economic features of natural resources. The number eventually needed may be many as neglected segments are studied and the complex interrelations of factors are clarified by new or the reappraisal of old scientific information. The rate of appearance of the succeeding issues should accord with the pressing need for the early establishment of an accurate and adequate foundation of basic facts on which effective programs can be formulated, sound policies established, and efficient management provided for our great natural resources.

Recent and highly productive research has clarified several vital parts of the mechanism and the nature and sequence of transformations in the process of photosynthesis, the most important of nature's processes, which directly or indirectly provides all man's food, the materials for most of his clothing and much of his shelter, and is the origin of the bulk of his energy.

Many features of the process are still unknown. Basic research now proceeding on a very limited scale is adding bit by bit to the structure of known facts and its completion to a state more in harmony with its importance could be accelerated if needed scientific personnel and facilities were made available for the full use of new techniques and the exploration of promising fields of inquiry.

A superstructure of applied research, including the economic along with the physical, erected on this expanding foundation of basic research could speed the process of converting the advancements in the basic sciences to their most productive results in meeting the needs of the Nation and of humanity.

The series of articles in this publication (I in the series) provides for the committees of Congress and others a generalized view of the present status of our knowledge of this process of photosynthesis and something of its significance for human welfare. Supplementing the articles describing the process are others dealing with the energy supply and the principal raw materials—carbon dioxide and water. The structure and processes of plants which are the "machines of photosynthesis" are also described, especially with regard to their water requirements.

Contributions to this document have been generously provided by professors of the Universities of Illinois, California, Wisconsin, and Utah, and of Stanford and Duke Universities.

Introduction

THE LEGISLATIVE RESPONSIBILITIES of the Committee on Interior and Insular Affairs of the House of Representatives of the United States encompass most of the broad field of natural resources. The committee's wide jurisdiction covers one of the most important areas of Federal functioning. The committee assignment includes programs and policies governing the public domain, the governing of extensive territorial and island possessions, the determination of Federal responsibility in water resource development, the manner of use and conservation of mineral resources, the methods of management of an extensive system of National Parks, and a number of other national resource problems.

The successful performance of these and other responsibilities of the committee would require an adequate collection of facts of the physical and economic features of these resources for guidance in achieving a sound natural resource foundation for the Nation's economy.

Under the sponsorship of the committee and its chairmen, progress has been made over the last 3 years on a program of reexamination of the scientific foundation in natural resources and various problems arising from the present lack of adequate knowledge of these resources.

The first phase of this study resulted in the introduction of two bills designed to strengthen the scientific foundation in natural resources. The first was "An Accelerated Surveying and Mapping Program" and the second " A Comprehensive Basic-Data Program for Water Resources." These bills and the description of the programs, on recommendation of the committee and approval by the House, were printed as House Document 706 of the Eighty-first Congress, under the general title of "A Program To Strengthen the Scientific Foundation in Natural Resources."

These reports revealed that not more than 25 percent of the surface of the United States had adequate topographic maps and only 10 percent satisfactory geological maps. Similar neglect was also found to prevail for needed basic data in water resources, a necessary prerequisite to the effective planning of large multiple purpose water management projects.

The completion of the mapping and basic data programs and other segments of a complete scientific program will require time. Even with the highest rate of acceleration that may be found feasible, adequate information will not be available for the planning of many projects that will be proposed for construction.

These deficiencies in the scientific foundation in natural resources create special and sometimes very great difficulties for those responsible for formulating programs and policies for developing the resources of this great country. There seems under these circumstances to be a special need for fostering preliminary or reconnaissance type surveys that will add as quickly as possible to our fragmentary knowledge of neglected phases of the physical and economic features of our resources. Great gains would come if the important features of unexplored resources could be established in a preliminary way and the meaning of all this for current and proposed projects made evident.

It was this set of circumstances that led to my request that Dr. J. R. Mahoney, senior specialist in natural resources in the Legislative Reference Service of the Library of Congress, explore the possibility of securing the cooperation of various scientists in a preliminary appraisal of these resources and provide guidance to the committee in fulfilling its responsibility. These positions of senior specialists provided for in the Congressional Reorganization Act of 1946 are available for special work with the committees of Congress or they may on their own initiative engage in research or other activity in preparation for problems which are or which may come before Congress.

In pursuit of this program the senior specialist in natural resources has obtained a ready response from scientists in various Federal agencies and from universities and other non-Federal agencies. Dr. Mahoney has the special ability and knack of getting the highest authorities, whether in government or of university faculties, in any given line to come out of the cloistered seclusion of their libraries and laboratories and compare their latest findings with their fellow workers on such vital matters. As stated elsewhere, this publication is a collection of papers by eminent authorities in leading universities. These authors have neither asked for nor received monetary compensation, but have voluntarily made their contributions to their Government for the advancement of science and the betterment of our Nation. For this I wish to make grateful acknowledgment and express my sincere appreciation.

The results of three of these studies are now available and are being printed for committee and other uses in a form similar to House Document 706. These reports are presented under the general title of *"The Physical and Economic Foundation of Natural Resources."*

The first is a collection of articles on the basic process of *photosynthesis*. All the articles in this collection have been prepared by personnel outside of Federal agencies. This course of action was adopted when it was reported that only a restricted amount of research in the basic features of photosynthesis, the most important of all the processes of nature, was under way in the United States. Nearly all of this research is concentrated in a few of the universities and

several of these have cooperated by making their findings and interpretations available for the use of Members of Congress and others.

Added to the overwhelming importance of photosynthesis for human welfare was the evidence that great progress had recently been made in determining the sequence of transformations and details of the process which, until recently, have baffled all efforts of scientists to identify and measure. There has been available to scientists in the last few years certain radioactive elements, an important byproduct of the atomic energy program. These, the isotopes of carbon, oxygen, phosphorous, and sulfur, have furnished effective tools for tracing the steps in the process of photosynthesis. A few of the basic features have now been identified and some processes have been photographed and measured. It is reasonable to suppose that with the fundamental features clarified that it will be possible to make rapid progress in using these scientific facts to improve our management of natural resources to better meet the basic needs of mankind.

Since sunlight and water are fundamental necessities for plant and animal life, one question arises—How can maximum results be obtained from the proper combination of these gifts of nature? A common notion prevailing is that water is merely a medium of transportation of the mineral plant food from the soil to the growing plants. That is indeed one of the functions of water in such biological processes, but the chemical and other contributions of water have not until recently been well understood. We are here asking up-to-date science to explain the total contribution of water and radiant energy of the sun in plant life and growth.

It was the splitting of the atom, giving man radioactive materials for his experimentation, that has enabled the scientists to inspect, analyze, and understand the mysteries in plant growth. Since much of the plant food for agricultural crops comes from the atmosphere, even more than from the soil, and the transformations are made possible by the radiant light of the sun, we will be better able to judge what crops can best utilize the possible combination of available water, sunshine, and other available resources. Such is the purpose of the following studies.

It would seem to be basically important that the committee follow these scientific advancements and determine as soon as it may be possible what significance there may be for the program and policies in the natural resource field under jurisdiction of the committee.

JOHN R. MURDOCK, *Chairman,*
Committee on Interior and Insular Affairs,
House of Representatives.

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The Physical and Economic Features of Photosynthesis

By J. R. MAHONEY, *Senior Specialist in Natural Resources, Legislative Reference Service, Library of Congress*

MUCH REMAINS FOR SCIENTISTS to complete descriptions of the mechanisms and processes of photosynthesis and to establish the techniques of most productive applications of their findings to improve and enlarge the useful products of the process. It is possible, however, to proceed with greater assurance than formerly in the appraisal of the requirements for more effective use of this great natural process.

The manner of conversion of the radiant energy of the sun to usable forms of chemical energy has been clarified even though much remains in discovering the exact mechanism through which it occurs and feasible ways of improving the efficiency of transformation.

Possibly the area of greatest relative advancement has been the discovery, through the use of ingenious techniques, of the path of carbon in photosynthesis and the demonstration of a number of its many combinations and functions in the process.

Other features in process of clarification are some of the many and vital functions of water. It has always been known that water is important in plant life, but there has been neglect of details and the manner of its specific uses.

It is now possible as a result of scientific advancements to focus attention more definitely on the means of securing a greater portion of the abundant supply of energy, enlarging the yearly withdrawals of basic raw materials from the gigantic reservoirs in which they are held, and in other specific ways bringing the potentials of this great process more nearly in harmony with the unfulfilled needs for its products.

While a comprehensive economic analysis of the process and its potentials must await further basic research, both physical and economic, a preliminary and necessarily fragmentary discussion of some features of the process as they relate to its economic position is presented in the following paragraphs.

Photosynthesis and Its Role in Nature

PHOTOSYNTHESIS, the process by which light energy from the sun is used by green plants to synthesize energy-rich compounds from carbon dioxide, water, and other substances, is the most important of all Nature's contributions to human welfare.

Plants are self-supporting from their own processes and products; but, in contrast, all animals, including man himself, are completely dependent upon this great fabricating process of photosynthesis. Plants supply the mechanism through which abundant raw materials and widely diffused energy are utilized to fabricate all the materials for their own varied needs and the basis of all animal life.

Plants convert light into chemical energy which may then be released to meet the many types of energy needs of both plants and animals. Man, with all of his technological attainments, has not developed an effective alternative method of converting this same abundant and only fractionally used light energy from the sun into manageable forms. Life on earth would not be possible, however, if green chlorophyll-bearing plants did not perform this task continuously and effectively.

This great energy-building process requires an appropriate mechanism through which light energy can be absorbed and converted immediately into chemical energy before it is transformed into heat. The energy utilized in splitting the water molecule—the first step in the process—must then

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be carried as hydrogen freed from its combination with oxygen in new but little-understood combinations to successive steps in the process of photosynthesis.

In the next step, the high-energy hydrogen reforms as water by removing from carbon dioxide a part of its oxygen content, and then additional hydrogen in a supplementary stream unites with the half-reduced carbon dioxide to provide the materials for the synthesis of sugar ($C_6H_{12}O_6$), the first product of photosynthesis. Successive transformations yield numerous intermediate and final products which provide plant structure, sustain growth, and furnish products for reoxidation to furnish the energy for all subsequent plant processes.

Beyond the green chlorophyll and primary products, increased concentrations of chemical energy can be achieved only through the partial or complete disintegration or transformation of the products of photosynthesis. All animals use these presynthesized materials, but they transform them in many ways for numerous life processes, body structure, and other vital functions.

Photosynthesis may also be described as a process which transforms abundant hydrogen, carbon, and oxygen from their small simple molecular structures (water and carbon dioxide) into larger, more-complex energy-rich plant products utilized by man for foods, fabrics, fuels, etc.

Photosynthesis, the course of which has not been completely explained, may not proceed along an identical path in all plant organisms from lowly diatoms to highly organized flowering plants; but the universal occurrence of chlorophyll in all plants, the use of the same source of energy, dependence on the same basic raw materials, and the similarity of the primary products, are strong presumptive evidence that the general characteristics, at least in the early stages of the process, may be the same throughout the plant world.

Beyond primary products of identical or close resemblance, however, differentation proceeds to varying intermediate substances and a myriad of divergent final products. This great mechanism supplying energy and form to all life is thus fed through a common channel, through which abundant materials are prepared and processed to form vital high-energy substances that meet a multitude of needs. These products, in the process of their use, generally find their way back to the substances from whence they originated to replenish reservoirs for successive and endless cycles of comparable production. These return streams constitute the life processes of plants, animals, and of man himself. The energy, however, is changed or dissipated through use and is unavailable for successive processes. Nor need it be, since the continuing over-all supply from the sun is superabundant and requires only its more complete capture to fill all human needs.

The chemical reactions which constitute these life processes build up molecules of carbohydrates, proteins, fats, vitamins, enzymes, and other constituents of living organisms which are combined, exchanged, or dissociated to form new substances or to release energy. Oxygen atoms released in photosynthesis or those comprising the great atmospheric oxygen reservoir (approximately 20 percent of the atmosphere) readily reunite with carbon, hydrogen, phosphorus, iron, and the other elements contained in plants and animals. In these processes of oxidation, water is regenerated, carbon dioxide reformed, nitrogen freed, minor mineral elements returned to the earth's crust and to the oceans, and energy is supplied for many life processes or heat or other forms of energy are generated.

Sooner or later, all living matter reverts to carbon dioxide, water, nitrogen, etc., and in the process the energy which it once contained is released as heat. This continuous cycle of life with its approximately matching rates of new products of photosynthesis and product use permits the elements brought into combination to be returned to their original raw-material reservoir for reuse in an endless chain. A small fraction of the products of past geological eras and its contained energy fortunately escaped dissipation and was preserved in energy-rich coal, petroleum, and other mineral fuel deposits. Protective layers of sediment have shielded these accumulations from the vast ocean of oxygen in the atmosphere thus preserving them for a multitude of vital uses.

The Place of Carbon in Photosynthesis

THE STRUCTURE AND FUNCTIONING of all forms of life on earth depend predominantly on the element carbon, by itself or in combination with other elements. Both plants and animals carry on their life functions amidst the changing chemical and energy manifestations of this vital element. The sum total of human wants supplied by carbon and its compounds is probably larger than the total of those supplied by all other elements combined.

Carbon is the most common and useful constituent of animal and vegetable matter. It is the most important element in our food and clothing, and generally also in our shelter. The use of carbon for fuel—coal, oil, gas, and wood—furnishes heat and power for nearly all the requirements of civilization. An enormous quantity of carbon in the form of coal, coke, and charcoal is used in the refining and processing of metals. It furnishes the heat, and usually the power, for the process. It also provides the means of removing oxygen from chemical combination with the metals. Carbon is the chief constituent of a wide variety of lubricants, drugs, dyes, explosives, auto finishes, pencils, photographic film, ink, automobile tires, paint, and varnish. These are but a few of the host of human necessities based on carbon and its compounds.

Carbon is the most versatile of the known 98 elements. It exists in forms as widely divergent as diamonds and graphite—essentially the hardest and the softest solids known. It possesses unique properties making possible its combination with almost all other elements. The existence of the greatest number and most complex carbon compounds, however, depends upon the capacity of carbon atoms to unite with other carbon atoms. These may be

attached to each other directly or linked through some other element.

The number of known carbon compounds has been variously estimated at between 300,000 and 1,000,000. The total number of known compounds without carbon for all the other 97 elements is probably no greater than 50,000. The number of possible compounds of carbon seems to be almost without limit.

Marked changes in the character and usefulness of products and the essence of many life reactions can result from even minute changes in the carbon content and from slight alterations in the carbon structure of the molecule.

The simplest compounds of carbon contain a single carbon atom in each molecule. However, there are carbon compounds known in which hundreds or even thousands of carbon atoms are present. Carbon dioxide, carbon monoxide, wood alcohol, and chloroform are examples of simple compounds. Large molecules are found in the cellulose of wood and cotton, in rubber, in the proteins of flesh and wool, in plastics and resins, and in oils, drugs, and dyes.

Carbon atoms form the skeleton or framework for many types of complex molecules. The shape of such a skeleton may be that of a single string of atoms, or of several strings tied together in various ways. Also, the carbon atoms may be held together in the form of rings. Upon such skeletons other atoms—those of hydrogen, chlorine, nitrogen, oxygen, and so forth—are held through electron-pair bonds in such numbers as to surround each carbon atom with eight electrons.

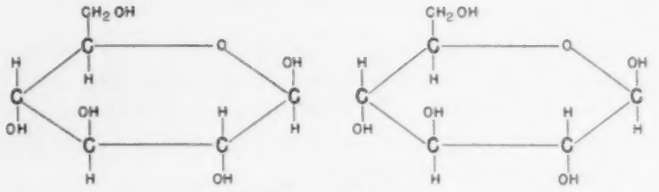
The reason for this capacity to combine with other elements is that sharing of electrons always leaves some carbon atom with fewer than eight electrons, and other carbon atoms can continue to add. In the diamond crystal each carbon atom in the interior of the mass is surrounded by four other carbon atoms, with a shared electron pair between each pair of atoms. It is this symmetry and compactness which makes diamonds so hard.

Reserves of Carbon Dioxide

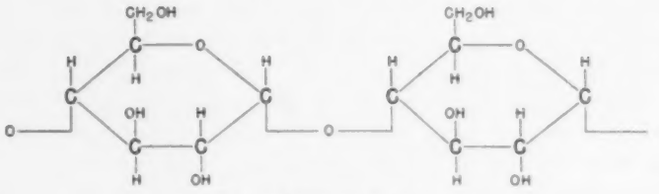
The supply of carbon for all the myriad products that serve the welfare of mankind has a single source: Carbon dioxide in the atmosphere and oceans. Carbon withdrawn from these great reservoirs flows through a single channel—the process of photosynthesis—and the power for driving forward the process also comes from a single source—the radiant energy of the sun.

The amounts of carbon dioxide withdrawn from these reservoirs is less than 2 percent for each yearly cycle, and fortunately these amounts are returned to the reservoirs in approximately the same quantities. Actually, the atmospheric reservoir of carbon dioxide is being progressively enriched through a return to the air of large quantities of carbon that have been entrapped for long geological periods in buried deposits of coal, petroleum, and other mineral fuels. These mineral fuels are now being withdrawn from their

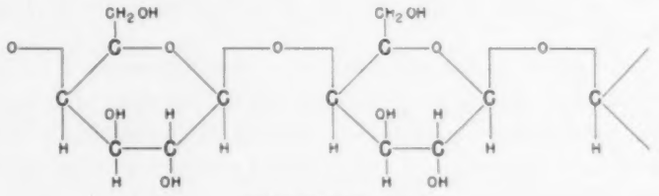
MOLECULES OF CARBON PRODUCTS



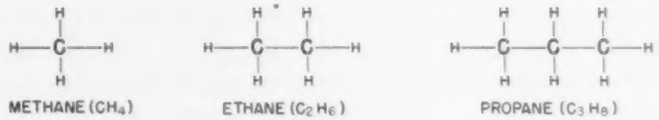
GLUCOSE (Sugar) ($C_6H_{12}O_6$)



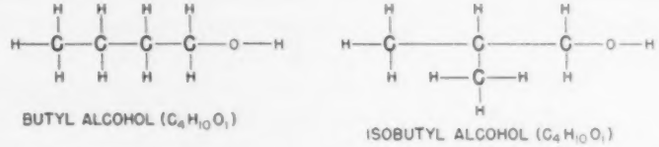
STARCH ($C_6H_{10}O_5$)



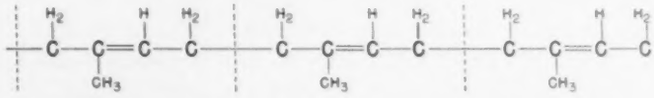
CELLULOSE ($C_6H_{10}O_5$)



METHANE (CH_4) ETHANE (C_2H_6) PROPANE (C_3H_8)



BUTYL ALCOHOL ($C_4H_{10}O_1$) ISOBUTYL ALCOHOL ($C_4H_{10}O_1$)



ISOPRENE (Natural Rubber) (C_5H_8) repeated 100,000 to 400,000 times

COMMON FATS

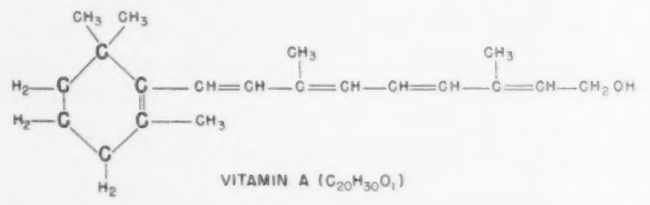
$(C_3H_5)(C_{17}H_{35}CO_2)_3$ STERIN (Beef, etc.)

$(C_3H_5)(C_{15}H_{31}CO_2)_3$ PALMITIN (Fruits, etc.)

$(C_3H_5)(C_{17}H_{33}CO_2)_3$ OLEIN (Olives, etc.)

CONSTITUENTS OF PROTEINS

$H_2NCH_2CO_2H$ $CH_3CHNH_2CO_2H$ $CH(NH_2)COOH$



VITAMIN A ($C_{20}H_{30}O_1$)

Sources: C–Carbon–(carbon dioxide–CO_2); H–Hydrogen–(water–H_2O); O–Oxygen–(CO_2 and H_2O); N–Nitrogen–(atmosphere)

subsurface confinement and reoxidized at rates which probably far exceed current entrapment of carbonaceous products in the earth's crust.

The carbon resources of the earth—the carbon content of the principal mineral fuel reserves, the quantities involved in the annual cycle of photosynthesis, and the annual transformation from mineral fuels to the atmosphere—are shown as estimates in the following table.

Reserves of carbon dioxide in the oceans are shown to be approximately 24 times the reserves in the atmosphere. Even though carbon dioxide gas constitutes only 0.031 percent of air by volume, it is 50 times the amount used annually by all the land plants of the earth. Less than 1 percent of the available reserve is required for all photosynthesis occurring in ocean waters. Any increase in withdrawal of carbon dioxide that depletes the reserve in the atmosphere would lead to replenishment from the far greater reserves of the ocean. These two great reserves are maintained in pressure equilibrium with each other, and in essence constitute a single reserve.

The return to the atmosphere of approximately 2 billion tons of carbon per year through the combustion of mineral fuels is effecting a gradual enrichment of the reserve. This would match the annual use in photosynthesis by land plants in approximately 8 years, but it would require 375 years to double the total carbon dioxide reserves in the atmosphere from this source and part of this would be absorbed by ocean waters.

The enormous size and the cyclical replenishment of these reserves of carbon match its countless forms and unlimited usefulness to make it the most useful element for the purposes of mankind and thus our greatest natural resource.

Water in Photosynthesis—Its Many Functions

In the process of photosynthesis water is used jointly with other resources, principally the radiant energy of the sun and carbon dioxide from the atmosphere and the oceans. Other elements are incorporated in the structure of plants, in their products, or serve in various vital plant functions. Altogether, these other elements comprise but a small portion of the total plant content. When all water diffused throughout the plant in liquid and vapor form is added to the water supplying hydrogen for chemical combinations, this vital substance becomes the dominant part of plants and the most used substance in the mechanism of photosynthesis.

A remarkable feat of power generation is accomplished as light entrapped by plant chlorophyll drives forward the molecular dissociation of water to provide varied streams of energy-laden hydrogen. Some to draw oxygen from its chemical combination in carbon dioxide. Some for chemical combinations of carbon, hydrogen, and oxygen as sugar and in succession an infinite variety of nature's most useful foods, structural materials, and energy supplies. Accumulations from energy streams of past geological periods are now available as mineral fuels—coal, petroleum, natural gas, and other hydrocarbons. These ancient products of photosynthesis were entrapped in the earth's subsurface formations and are now available to drive the machines of modern industry and furnish heat and power for many purposes.

Water provides the fluid medium in which all chemical and energy transformations are consummated within the plant. Instantaneous replenishment of water supplies consumed or dissipated in the process is necessary for the most effective operation of nature's great factory.

Carbon Resources of the Earth (in net tons)

	Reserves	Annual use in photosynthesis	Return to reserves through respiration and combustion
Oceans	18, 000, 000, 000, 000	135, 000, 000, 000	135, 000, 000, 000
Atmosphere	750, 000, 000, 000	15, 000, 000, 000	15, 000, 000, 000
Mineral fuels:			
World total	4, 460, 000, 000, 000		2, 000, 000, 000
Types of fuels:			
Coal	4, 400, 000, 000, 000		1, 400, 000, 000
Petroleum	11, 000, 000, 000		400, 000, 000
Oil shale	33, 000, 000, 000		
Natural gas and other	16, 000, 000, 000		200, 000, 000
United States total	1, 732, 500, 000, 000		750, 000, 000
Coal	1, 700, 000, 000, 000		430, 000, 000
Petroleum	3, 500, 000, 000		215, 000, 000
Oil shale	25, 000, 000, 000		
Natural gas	4, 000, 000, 000		105, 000, 000

Water modifies temperatures on leaf surfaces by reducing maximum and, under certain circumstances, increasing the minimum temperatures. The dissipation of excess heat through vaporization of water from overheated leaf surfaces and in a reverse process the release of heat through condensation of water vapor to a liquid dew provides a more appropriate setting for photosynthesis.

Water provides the medium of transportation for most plant processes as it moves in an unbroken chain from the roots through the plant structure to the seat of photosynthesis in the leaves, carrying in solution supplementary elements drawn from the soil. In a reverse flow, the primary and secondary products of photosynthesis are distributed throughout the plant for structural growth, accumulation as harvestable products, or to supply plant energy requirements.

A second energy supply is provided by the change in state of water, from liquid to vapor, streaming through the stomata of the leaves to the atmosphere and providing the suction power to pull water through roots and stems to the leaves. While the source of energy is light from the sun it is the changing states of water which constitute the medium of energy transfer to operate the pumping mechanism provided by the structure of plants.

This overwhelming importance of water for the most vital processes in photosynthesis is without parallel in any fabrication process designed and carried on under human control. For a single element or factor in a typical manufacturing plant to achieve comparable importance with water in photosynthesis, it must provide an equivalent to the following:

Supply one of the major raw materials.

Provide the mechanism through which all incoming power and energy supplies are converted into appropriate forms for use in subsequent plant processes and for incorporation as stored energy in all finished products.

Furnish an equivalent to the mixing vats, and metallurgical vessels for raw material conversion and transformation from semifinished to finished products.

Provide complete conveyor and transportation systems—trucks, railroads for raw material collection, continuous belt conveyors and other facilities—to move raw materials and intermediate products through the plant and finished materials to points of storage or shipment.

Supply mechanisms to modify temperature extremes for improved plant operation, by dissipation of excess heat and by raising minimum temperatures.

Constitute an important part of all plant structures and facilities.

And finally, be freely interchangeable among several coexisting forms—liquid, vapor, liquid film, and as a material of inclusion in various facilities and products.

These combined vital functions supplied by water in the process of photosynthesis, make water management the dominant means of controlling and improving the entire process. It is the only one of the three major factors—energy, carbon dioxide, water—subject to control.

The pattern of water requirements is determined primarily by variations in the flow of light energy from the sun. Extreme variations and sometimes rapid changes in the light supply occur within each daily cycle between the maximum at noonday and the minimum at night. Of even greater extremes are the seasonal variations in both the temperate and frigid zones.

Any break in the water column between the roots and the leaves means injury or even death to the plant. Plants must, therefore, be equipped with a mechanism capable of reducing the loss or conserving the supply of water to insure continuity in all vital functions.

Water supply on land surfaces is seldom in exact harmony with plant needs and over most of the earth's surface numerous ingenious mechanisms have been developed by plants to survive periods of deficiency and compensate for any lack of harmony between water supply and water needs. The infinite varieties of plant types, each with a mechanism of adjustment to its typical water supply, have developed through natural and artificial selection to fit each its own water environment.

Economics of Water Use in Photosynthesis

The extreme variations in the range of physical and economic results of the use of water in photosynthesis are so great—ranging between one and several thousand—that the resulting wide range of value situations are quite unlike those of other substances. Tremendous quantities of water are sometimes consumed in photosynthesis with little or no economic results, while in its highest controlled uses slight additional amounts of water at the right time may increase the useful results several fold.

In general, the highest achievable results from the use of water are more directly related to the manner of its use rather than to quantities. Under many circumstances, a smaller supply of water effectively distributed will produce greater results than a larger supply with deficiencies in distribution. The highest uses of water in photosynthesis are achievable only under conditions of careful synchronization with plant needs. These needs for water are determined primarily by variations in meteorological forces, principally light and heat, which are subject to extensive daily and seasonal variations.

The actual technique of water application to meet these meteorological variations has been formulated only in a general way, but information already is sufficient to foreshadow great potentials when these techniques have been more completely developed. A great unknown is the increased productive results attainable when plants have been selected and progressively adjusted to achieve maximum photosynthesis under various types of controlled water environments.

Importance of Plant Structure

Attainable physical and economic results of photosynthesis are directly related to the structure of the plant, but since most plants have progressively adjusted to an en-

vironment of uncertain water supply, their present structure generally restricts the total possible products to a fraction of the potential as measured by the energy and raw materials available even when water supply is made completely responsive to their requirements.

There is great need for a selective adaptation of plants to permit more nearly the maximum physical volume of products under well-managed systems of irrigation, supplementary irrigation, or natural and controlled water environments. These need not be heavy water-consuming plants, but their structure must provide for continuous or accelerated rates of photosynthesis through more complete responsiveness to existing meteorological forces. The intricate and elaborate mechanisms of most plants permit retardation or termination of the processes of photosynthesis in order to insure an unbroken water column between the roots and the liquid medium permeating the leaves. This specialized structure that insures the continuity of their life processes is often at the expense of the physical product of photosynthesis.

Aside from an increase in the physical volume of harvestable products of photosynthesis possible under a balanced water supply and from plants capable of responding more fully to the potentials, significance can also attach to improvements in the quality of products.

Recent clarification of the composition of initial products and in the sequences of the processes of photosynthesis may provide the necessary basis for developing controls over the secondary and final products in the interest of greater usefulness to human needs. There seems evidence of great potentials when these techniques are perfected and facilities for controlled application of water to meet the variable daily and seasonal water needs of the plants are provided. For some situations, exact apportionment may require even a smaller total amount of water and in other circumstances only a slight addition to amounts currently available from Nature's own distribution will be required.

All this justifies the conclusion that facilities and mechanisms permitting carefully controlled application of water are more important than mere increases in the quantity. There may be many situations where small supplies of water under exact control will yield superior results to supplies several times as large, where applications cannot be synchronized with plant needs.

Primary emphasis should, therefore, be concentrated on the identification of favorable facilities of water control, chiefly effective ground-water reservoirs and the appraisal of all factors affecting the conservation of water required to fill the reservoirs. Conservation will require, in many cases, transfer to such reservoirs of water now used in less productive ways.

When the full techniques of water-resource management have been developed, the relocations of productive activity may entail important alterations in the geographical pattern of crop production. These possibilities establish an imperative need for complete exploration of all situations where water can be available in a continuous unfailing supply. This must be followed or accompanied by the research and activities that will select and adapt plants to each situation so that full-scale use can be made of available resources.

Photosynthesis—Historical Development of Scientific Interpretation and Significance of the Process

By EUGENE I. RABINOWITCH, *Research Professor of Botany, University of Illinois*

PHYSIOLOGICALLY SPEAKING, all animals on land and in the sea, including man, are but a brood of parasites living off the great body of the plant kingdom. If plants could express themselves, they would probably have the same low opinion of animals as we have of fleas and tapeworms—organisms that lazily depend on others for survival.

We cannot conceive of life existing on the earth or on any other planet without plants, our main reason for suspecting that there is life on Mars is the greenish coloration of certain parts of that planet. So far as we know, green plants alone are able to produce the stuff of life—proteins, sugars, fats—from stable inorganic materials, with no other help but the abundantly flowing light of the sun. This is the process called photosynthesis. Scientists have not yet been able to imitate it in the laboratory, even on a microscopic scale, but stately green trees and microscopic diatoms alike achieve it every day on a gigantic scale. Each year, the plants of the earth combine about 150 billion tons of carbon with 25 billion tons of hydrogen, and set free 400 billion tons of oxygen. Few are aware, incidentally, that over one-half—perhaps as much as 90 percent—of this giant chemical industry is carried on under the surface of the ocean, by free-swimming microscopic algae.

A small fraction of the organic material synthesized by land plants is later utilized as food by land animals. A much larger amount is used in the respiration and other life activities of the plants themselves. The greatest part, however, is decomposed into water, carbon dioxide, and mineral salts by the decay of leaves and dead plants. Under certain climatic and geological conditions, this decay is halted, huge masses of half-decayed plant material then accumulate for millions of years, under a protective layer of rock or silt, eventually to become peat or coal.

In endlessly repeated cycles, the atoms of carbon, oxygen, and hydrogen come from the atmoshpere and the hydrosphere (the world sea) into the biosphere (the thin layer of living things on the earth surface and in the upper part of the ocean). After a tour of duty in the unstable organic world, which may last seconds or millions of years, they return to the stable equilibrium of inorganic nature.

The organization of atoms in the biosphere is distinguished from that of the inorganic world by two characteristics: chemical complexity and high energy. In the inorganic world, we find carbon in the simple molecules of carbon dioxide (CO_2), which, with water (H_2O), forms carbonic acid (H_2CO_3), and in the ions derived from the latter (CO_3 and HCO_3). In striking contrast is the complexity of even the simplest organic compounds, such as glucose ($C_6H_{12}O_6$)—not to speak of the enormous and intricate structures which are the molecules of proteins. It is this complexity that permits the almost infinite variability of organic matter. One thing, however, all the multifarious organic molecules have in common: they are all combustible, i. e., they have an affinity for oxygen. When oxidized, they release an average of about 100 kilocalories of heat for each 10 grams of carbon they contain. Thus, all organic matter contains a considerable amount of potential chemical energy, available for conversion into mechanical motion, heat, eletericity, or light by gradual or sudden combination with oxygen. Such oxidations are the mainspring of life; without them, no heart could beat, no plant could grow upward defying gravity, no amoeba could swim, no sensation could speed along a nerve, no thought could flash in the human brain. Certain lower organisms can exist using sources of chemical energy not involving free oxygen, such as fermentation, but these are merely "exceptions that prove the rule."

Photosynthesis by plants is the process by which matter is brought up from the simplicity and inertness of the inorganic world to the complexity and reactivity that are the essence of life. The process is not only a marvel of synthetic chemical skill, but also a tour de force of power engineering. When plant physiologists and organic chemists study photosynthesis, they are struck by the chemical feat of manufacturing sugar from carbon dioxide and water. When physicists or photochemists contemplate the same phenomenon, they are awed by the conversion of stable, chemically inert matter into unstable, energy-rich forms by means of an agent as mild as visible light.

Historical Beginnings

The story of photosynthesis begins with Joseph Priestley, who announced in 1772:

> I have been so happy as by accident to hit upon a method of restoring air which has been injured by the burning of candles and to have discovered at least one of the restoratives which Nature employs for this purpose. It is vegetation. One might have imagined that since common air is necessary to vegetable as well as to animal life, both plants and animals had affected it in the same manner; and I own that I had that expectation when I first put a sprig of mint into a glass jar

standing inverted in a vessel of water; but when it had continued growing there for some months, I found that the air would neither extinguish a candle, nor was it at all inconvenient to a mouse which I put into it.

In these words Priestley, a religious reformer, philosopher, and spare-time naturalist of the age of enlightenment, described one of the most momentous observations in the history of experimental biology: the discovery of the capacity of plants to produce free oxygen.

Seven years later Jan Ingen-Housz, Dutch physician to the Austrian Empress Maria Theresa, who was at that time working in England, noticed another aspect of the same phenomenon. Ingen-Housz wrote in 1779:

I observed that plants not only have a faculty to correct bad air in 6 or 10 days by growing in it, as the experiments of Dr. Priestley indicates, but that they perform this important office in a complete manner in a few hours; that this wonderful operation is by no means owing to the vegetation of the plant, but to the influence of the light of the sun upon the plant. * * * I found that this operation of the plants is more or less brisk in proportion to the clearness of the day and the exposition of the plants; diminishes toward the close of the day, and ceases entirely at sunset; that this office is not performed by the whole plant, but only by the leaves and the green stalks. * * *

Thus was discovered the necessity to photosynthesis of light and of the green pigment, chlorophyll. In 1782, a Geneva pastor named Jean Senebier added another important requirement: "fixed air" (carbon dioxide). Only three cubic centimeters of carbon dioxide are present in 10 liters of air, but take this small amount away and all oxygen production in light will stop.

The old and persistent theory of "humus nutrition" of plants (even now many still believe that "good, black earth" provides plants with organic nutrients, though in fact it supplies only inorganic minerals), had been shaken already a hundred years before Priestley, when the Flemish physician and chemist Jan van Helmont grew a large tree in a bucket of earth, and found that the weight of the earth was not lessened by an ounce. The time was now ripe for a new and better explanation of the origin of vegetable matter. The discoveries of Priestley, Ingen-Housz, and Senebier, interpreted in the new chemical language of Antoine Lavoisier, had indicated that green plants, exposed to light, absorb carbon dioxide and liberate oxygen. Inevitably, the question arose: What do they do with the other constituent of carbon dioxide—carbon? In 1796, Ingen-Housz supplied the answer: This carbon, he said, is used for plant nutrition; photosynthesis, he proclaimed, is not merely "epuration of air" for the benefit of animals and man, but, first of all, carbon assimilation for the benefit of the plants themselves.

An important ingredient in the chemistry of photosynthesis was still missing; the omission was corrected in 1804 by another learned citizen of the city of Geneva, Nicholas Theodore de Saussure. He found that, in addition to carbon dioxide, water also enters into the photosynthetic production of organic matter:

$$\text{Carbon dioxide} + \text{water} \xrightarrow[\text{light}]{\text{green plants}} \text{organic matter} + \text{oxygen}$$

FIGURE 1.—*Tree secures little of its substance from earth.*

In the absence of light, or in parts of the plant that are not green, the process is reversed: respiration of the plant produces water and carbon dioxide from organic matter and oxygen.

Thus by about 1800, the chemical nature of photosynthesis was established, except for one detail—the recognition that the organic matter primarily manufactured in photosynthesis is a carbohydrate. This class of compounds is made up of carbon combined with hydrogen and oxygen, in the same ratio as in water. In the chemist's shorthand, carbohydrates may be written $C_n(H_2O)_n$. All sugars, as well as starch and cellulose, are carbohydrates. The conclusion that a compound of this type must be the first product of photosynthesis was reached by plant physiologists in about 1850, on the basis of determinations of the relative amounts of carbon dioxide and oxygen exchanged in photosynthesis, and of observations of the formation of starch in illuminated leaves.

Julius Robert Mayer, the German doctor who discovered the principle of conservation of energy, was the first to note the fundamental physical function of photosynthesis—the conversion of light energy into chemical energy. He wrote in 1845:

Nature set herself the task to catch in flight the light streaming toward the earth, and to store this, the most evasive of all forces, by converting it into an immobile form. To achieve this, she has covered the earth's crust with organisms, which, while living, take up the sunlight and use its force to add continuously to a sum of chemical difference.

These organisms are the plants: the plant world forms a reservoir in which the volatile sun rays are fixed and ingeniously laid down for later use; a providential economic measure, to which the very physical existence of the human race is inexorably bound.

With this perception it became clear that photosynthesis by green plants, in addition to being the ultimate source of all food on earth, also is the only source of animal energy. Through its products—wood, coal, oil, natural gas, and peat—photosynthesis becomes also the main source of our industrial power, heat, and light; indeed, it satisfies all the energy requirements of modern civilization except the small fraction—less than 1 percent—which is met by water power. In future, some of these requirements may be fulfilled by nuclear disintegrations, or by nonbiological conversion of sunlight into thermal, mechanical or electrical energy, or by the utilization of ocean currents or tides. At present, the energy derived from all these sources is neglible; and it is unlikely that any of them will ever displace photosynthesis from its predominant position in the energy household of mankind.

The Challenge to Science

Since the discoveries of Priestley, Ingen-Housz, Senebier and Mayer, hundreds of botanists, chemists, and physicists have studied photosynthesis. Thousands of papers have been published on its different aspects. And yet we still do not fully understand photosynthesis and cannot repeat it outside the plant cell—a vexing situation and a continuing challenge.

The biochemist feels that he "understands" a chemical process in the living cell if he knows its successive stages, the intermediate compounds that are formed and the enzymes (biological catalysts) that make the individual reaction steps possible. This knowledge he achieves by taking the biochemical apparatus apart and putting it together again. His ultimate aim is to imitate a life process, in the test tube, such as respiration or the conversion of carbohydrates to fats, and to describe each step in detail by chemical equations. This aim is rarely achieved in full; but often we know at least the main stages of a metabolic process and can repeat them outside the living cell. As an example, we know well the first steps in the breakdown of glucose (dextrose) in animal respiration: they are the formation of a molecule, of glucose diphosphate ester, which is then split into two molecules of triose monophosphate ester. We know the enzymes involved in these reactions and can repeat them in the test tube. It is true that we do not understand how these enzymes produce their miraculous, reaction-stimulating effects; but this is a more advanced problem: before it can be tackled, the reaction steps must be identified, and their specific enzymes isolated and identified.

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In the case of photosynthesis, we know very little about the individual reaction steps, and even less about the catalysts which make them possible. We can prepare extracts from plant cells containing chlorophyll and other pigments, which are present wherever photosynthesis goes on; but these extracts prove incapable of bringing about, not only complete photosynthesis, but even simpler reactions which could be considered as steps in photosynthesis. We may decide that chemical methods of fractionating the plant cell contents are too drastic, and attempt instead to take the cell apart by mechanical means. We take a giant green cell, such as are formed by some algae, and prick it with a needle in an attempt to reach its interior. Immediately, photosynthesis ceases.

Thus we find ourselves in the position of being asked to find out how an automobile operates without being permitted to lift the hood. We see that the engine consumes carbon dioxide and water, that it produces an exhaust gas (oxygen) and stores chemical energy in the form of carbohydrates. We can look at the instrument board and note how the speed of the motor's revolution depends on the supply of fuel, temperature of the coolant, and other factors which we can control; however there is not much hope that we shall ever be able to deduce from such circumstantial evidence how the motor is constructed and what chemical reactions take place in its cylinders.

Recent Developments

This was the situation in the study of photosynthesis until quite recently. There was no known way of dismantling the biochemical apparatus of photosynthesizing plants and studying its parts separately. We were facing, it seemed, an "all or nothing" situation: either we had a living cell, engaged in complete photosynthesis or an agglomeration of broken parts or isolated chemical compounds, with no indication of what role, if any, these parts or compounds had played in photosynthesis while the cell was alive.

Within the last few years the situation has changed. The problem looks less forbidding. Some progress has come from better general understanding of the mechanism of chemical and, in particular, photochemical reactions. Some has come from the improvement of old experimental methods and the development of new ones, exact rate measurements by electrochemical and manometric devices, radioactive tracers, quantitative spectrophotometry. None of these methods, not even the glamorous radioactive tracers, can lead to an immediate solution of all the secrets of photosynthesis, but all of them together promise progress toward the understanding of photosynthesis in vivo, and its imitation in vitro. Beyond these two achievements, there beckon grandiose technological goals: synthetic production of organic materials and power supply from sunlight.

The main result of recent studies is the realization that photosynthesis consists of two main stages, which can roughly be called the stage of energy storage and the stage of organic synthesis. In the first stage, the light energy

absorbed by chlorophyll (and by other, mostly yellow or red pigments, contained in many if not all photosynthesizing plant cells), is applied to the removal of hydrogen atoms from their stable association with oxygen atoms in water (leaving free oxygen behind), transferring these atoms to an as yet unknown "acceptor"—a molecule which holds hydrogen loosely, and readily supplies it to the second stage of the process. This stage consists of a sequence of chemical transformations, catalyzed by unknown enzymes, into which carbon dioxide and hydrogen atoms are fed on one end, and carbohydrate comes out on the other end. The exact nature of the reactions in this sequence is as yet unknown, but its general outline has begun to emerge.

Calvin and Benson and their co-workers at the Radiation Laboratory at the University of California at Berkeley, and Gaffron, Fager and their co-workers at the University of Chicago, have fed to plants carbon dioxide containing radioactive carbon, killed them, and isolated the organic compounds into which the isotopic tracer was first incorporated. In this manner, the first product of carbon dioxide transformation in photosynthesis was identified at Berkeley; the finding was later confirmed in Chicago. This, the first reliable identification of an intermediate of photosynthesis, is an important milestone. The hitherto elusive intermediate turned out to be glyceric acid (more exactly, a phosphate ester of this acid), a well-known, simple organic compound. It is situated halfway between carbon dioxide and sugar, both from the point of view of the length of the carbon chain in its molecule (three carbon atoms in glyceric acid, as compared to one in carbon dioxide and six in sugar), and from the point of view of its saturation with hydrogen (no hydrogen in carbon dioxide, three hydrogen atoms to two oxygen atoms in glyceric acid, six hydrogen atoms to three oxygen atoms in carbohydrates). With this first success, the unraveling of the chemical transformations that carbon undergoes in the conversion of carbon dioxide to organic matter, is off to a promising start, after many decades of frustration.

The study of the "powerhouse" of photosynthesis (as contrasted to its "chemical factory"), also looks more hopeful today. Ten years ago, R. Hill, in Cambridge (England), found that if green plant cells are broken to pieces, the fragments containing chlorophyll still can produce oxygen from water in light, provided they are supplied with a "substitute acceptor" for hydrogen, instead of the normal acceptor, which is carbon dioxide. This means that while the chemical factory is blown up in the destruction of the cells, the powerhouse has remained essentially intact. From Hill's discovery stemmed a series of investigations, by French, Holt and others at the University of Minnesota, by Warburg in Germany, and many others, in which the energy stored by illuminated fragments of green plants, was applied to different chemical uses. These studies are now approaching culmination in an apparently succesful attempt by Ochoa and co-workers at New York University, and by Franck, Gaffron and their co-workers at Chicago, to use the "light powerhouse," salvaged after the breaking up of green cells, to produce, in an artificial mixture of chemicals and enzymes, a transformation similar to that which carbon dioxide undergoes in photosynthesis. Here, too, science appears to be on the threshold of important new revelations.

Another promising step was made by a Russian photochemist, Krassnovsky. He proved, in 1948, that chlorophyll extracts in certain organic solvents can be used to produce, in light, chemical reactions which, though involving no liberation of oxygen from water, and no conversion of carbon dioxide to organic matter, nevertheless have something in common with photosynthesis—namely that in them, too, light energy is converted into chemical energy. We do not know yet how significant these findings will prove for the achievement of our ultimate aim of taking the photosynthesis apparatus apart and putting it together again; but the prospects seem engaging.

One theoretically and practically equally important question about the energy-storing plant in photosynthesis is: How efficient is this plant? In other words, what proportion of light energy, taken up by chlorophyll, is converted into chemical energy under the most favorable conditions?

Thirty years ago, this question was first investigated by the German biochemist, Otto Warburg. The answer was: up to 75 percent—an extraordinarily high efficiency for the operation of a complex chemical machinery, in each part of which some energy could be expected to be wasted by "friction." When American investigators (first at the University of Wisconsin and then at the Carnegie Institution of Plant Physiology at Stanford, Calif.) tried to repeat Warburg's experiments in 1938–40, they obtained a different answer: The conversion efficiency found by them was at best, 25 or 30 percent. Since 1948, Warburg (recently, in collaboration with the American biochemist, Dean Burk), has not only reaffirmed his original findings, but beyond that, found that the conversion of practically 100 percent of absorbed light into chemical energy is possible under certain conditions. These conclusions are contested by several American investigators, notably R. Emerson at the University of Illinois. They doubt whether the measurements from which the high efficiencies were derived, gave a correct picture of the efficiency of steady photosynthesis, involving as they did, alternation of short periods of darkness and light. They see these measurements influenced by transitional phenomena, either in the plant cells or in the measuring devices. It is to be hoped that general agreement will soon be reached on this point. The maximum efficiency of photosynthesis which can be reached in the laboratory, cannot be and will probably never be approached under agricultural conditions; but the knowledge of this maximum efficiency provides a standard against which to measure practical achievements, and is important for the theoretical understanding of the photochemical processes in photosynthesis.

Photosynthesis—Mechanisms and Processes of Energy Transfer, Carbon Fixation, and Product Synthesis

By Melvin Calvin, *Director, Radiation Laboratory, University of California, Berkeley* [1]

Photosynthesis is the biochemical process whereby green plants utilize the energy of light to convert carbon dioxide gas and water to carbohydrates or other reduced carbon compounds and oxygen gas. Reduced carbon compounds are those substances which can be burned either by a fire or by the metabolism of an animal or other organism to give carbon dioxide, water, and energy. The chemical equation which denotes the process of photosynthesis is usually written:

$$(1)\qquad \underset{\text{carbon dioxide}}{CO_2} + \underset{\text{water}}{H_2O} + \text{light energy} \longrightarrow \underset{\text{carbohydrate}}{\{CH_2O\}} + \underset{\text{oxygen gas}}{O_2}$$

[1] The Photosynthesis Laboratory Group is composed of the following personnel: Melvin Calvin, Andrew A. Benson, James A. Bassham, Victoria H. Lynch, and William Stepka. The work described in this paper was sponsored by the United States Atomic Energy Commission.

while the over-all process of burning or metabolic combustion is just the reverse, namely:

$$(2)\qquad \underset{\text{carbohydrate}}{\{CH_2O\}} + \underset{\text{oxygen}}{O_2} \longrightarrow \underset{\text{carbon dioxide}}{CO_2} + \underset{\text{water}}{H_2O} + \text{energy (many varieties)}$$

Thus, it is seen that photosynthesis is an energy storage process which makes possible the conversion of radiant energy to forms of energy which can be more easily utilized.

In a discussion of the scope and importance of the process it is useful to consider briefly the energy available on the earth and the present utilization of this energy. The principal primary forms of available energy are radiant solar, nuclear, and tidal. No discussion of the latter two will be attempted here. It suffices to say that virtually all energy

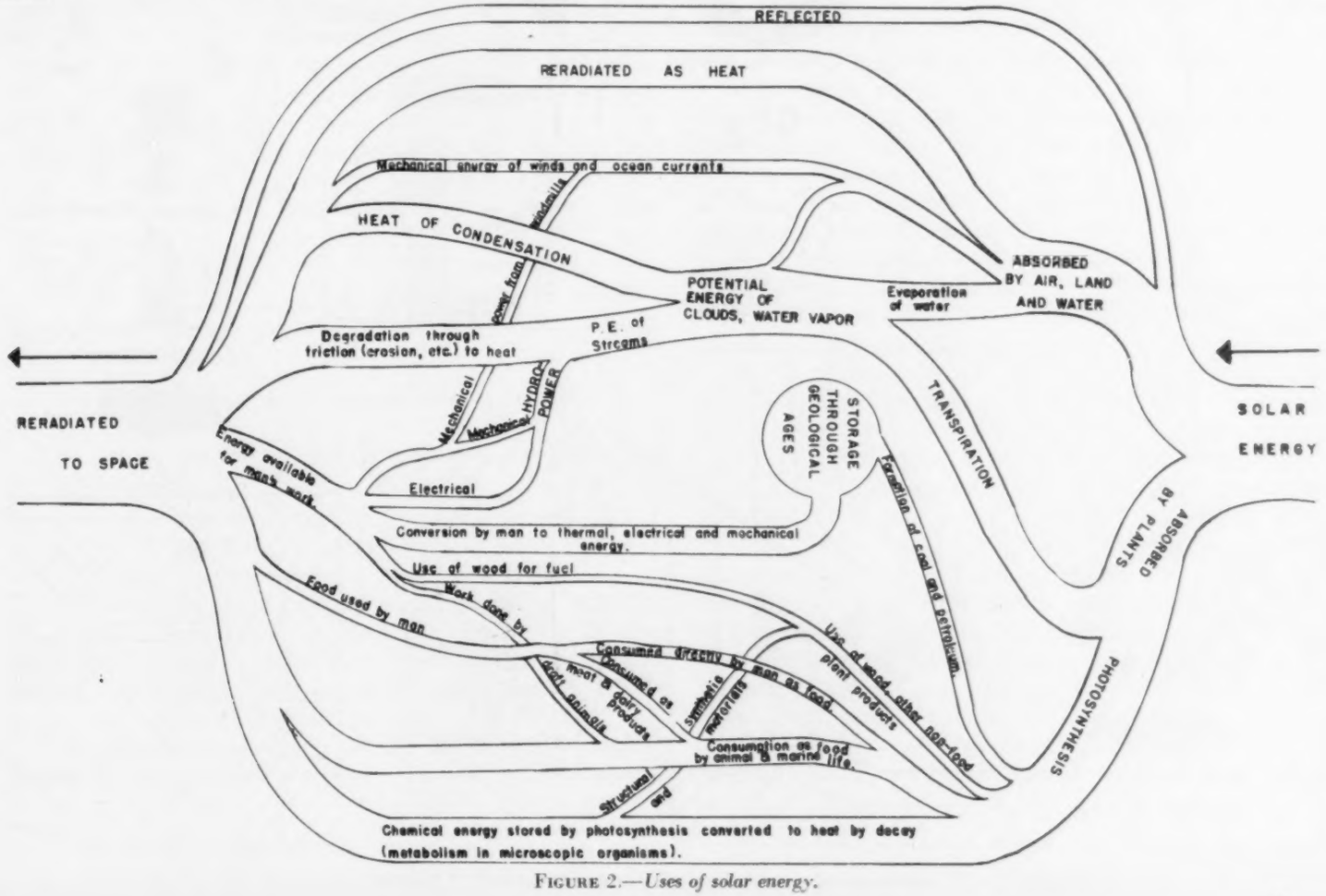

Figure 2.—*Uses of solar energy.*

used by man is derived from radiant solar energy and that this will probably always be the case. Even the uncontrolled release of energy in an exploding atomic bomb is minute compared to the incident radiant solar energy per second on the earth's surface.

Energy for Photosynthesis

The ways in which radiant solar energy is used are indicated in figure 2. The widths of a given energy channel should not be taken as a quantitative measure of the amount of energy used by that channel. Of the incident solar energy, one part is reflected directly as visible light (like moonlight or the reflected light we see from other planets), a second part is absorbed and converted to heat energy by inorganic material (earth, water, and air), while a third part is absorbed by the pigments of green plants. The transformations of energy absorbed by inorganic material can be seen from figure 2. Some is reradiated as heat while another part is used in the making of weather, the flow of wind and water over the earth's surface. Some of the energy of this flow is

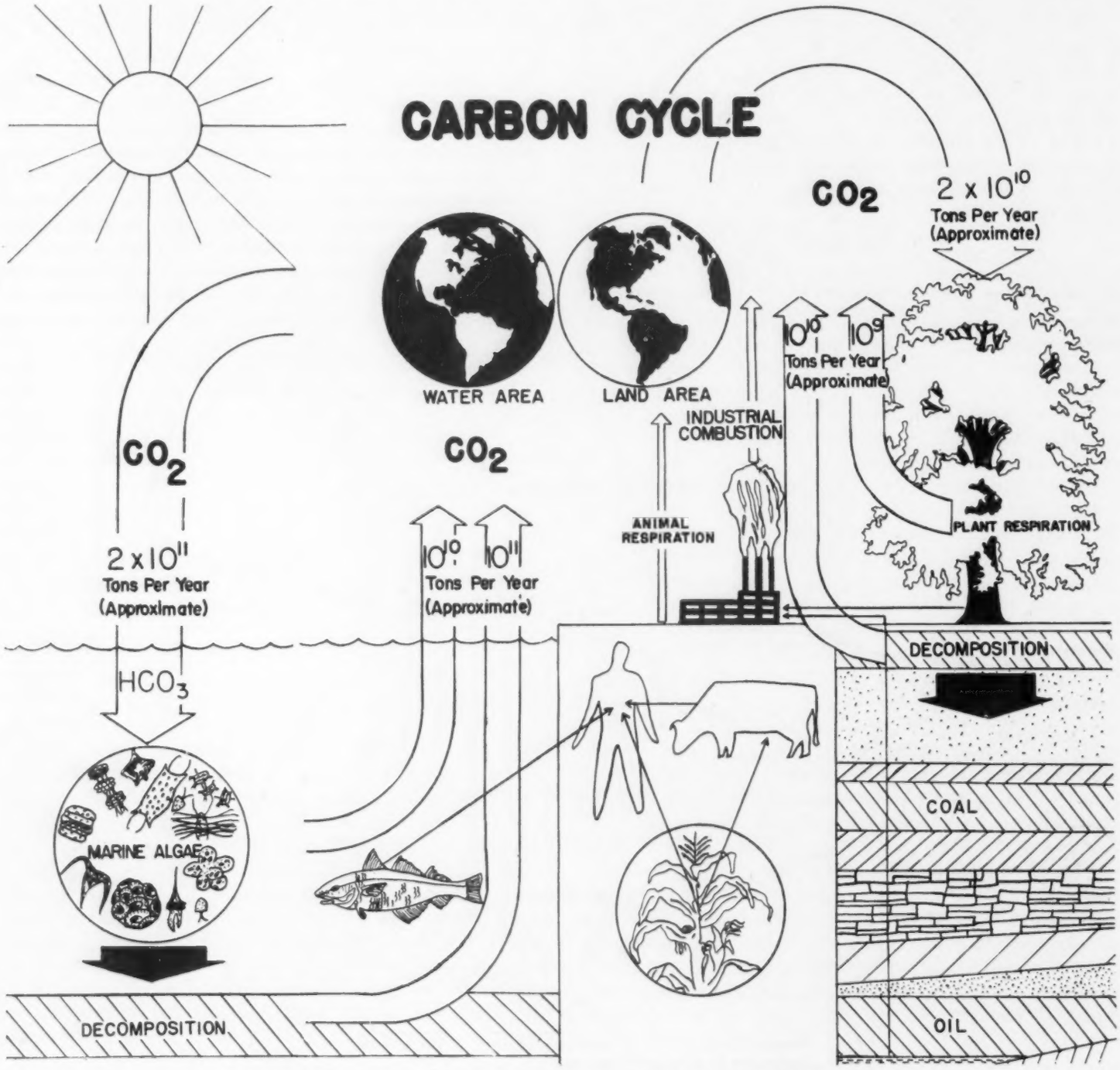

FIGURE 3.—*The carbon cycle (reproduced through courtesy of the editors of Scientific American).*

converted to mechanical and electrical energy by man and all is eventually degraded to heat and reradiated to space.

Of the energy absorbed by the plants, part is used for evaporation of water from the plant leaf, a process wnich is called transpiration, while the rest is used in the process of photosynthesis.

Of the energy stored by photosynthesis, a large part is released again through decay of organic materials by microorganisms and thus never becomes available to man. From the remaining portion comes all of our food, most of our fuels, and much of our structural materials.

The chemical statement of photosynthesis (equation (1)) which was given in the introduction is thought to be comprised of two processes. The first of these is the photochemical process discussed above, which is expressed chemically as follows:

(3) Light energy + $2H_2O$ + $2R \longrightarrow O_2$ + $2RH_2$

water; oxidized energy carrier; oxygen; reduced energy carrier

In this process, the energy of the sun (or artificial light) is absorbed by chlorophyll and used by the plant to strip the hydrogen atoms from the oxygen of water, forming free oxygen (O_2) and reduced energy-carrying compounds (RH_2). The decomposition of water by light thus produces compounds containing sufficient chemical energy to supply the energy required by all the subsequent chemical reactions performed by the plant. That the oxygen comes from the water rather than carbon dioxide was shown by the experiments with oxygen 18. Water containing the labeled oxygen was fed to the plant, and it was noted that the oxygen as it evolved had the isotopic composition of the water rather than that of the carbon dioxide. This means, of course, that the oxygen of the carbon dioxide must pass through the water stage before it is evolved as gaseous oxygen. This was one question answered by the isotope technique. This technique, as applied to carbon, will be discussed in more detail below.

Mechanism of Carbon Reduction

The second process in photosynthesis can be represented by the equation:

(4) CO_2 + $2RH_2 \longrightarrow [CH_2O]$ + $2R$ + H_2O

carbon dioxide; reduced energy carrier; carbohydrate; water

In this way R, which represents a hypothetical fragment of an organic compound, is regenerated and can be used again in the photochemical step, while the energy derived from the breakdown of RH_2 is used to reduce carbon dioxide to reduced carbon compounds (fig. 4.)

A diagrammatic summary of the entire photosynthetic process represented by the sum of equations 3 and 4 is shown in figure 4. The left-hand portion of the chart performs the initial conversion of solar energy into chemical energy in the form of reduced compounds (RH_2) and gaseous molecular oxygen (O_2). This is the process described by equation 3. The right-hand part of the diagram performs the reduction of carbon dioxide to the wide variety of plant materials, including the common foodstuffs of man and animals. This is the process described by equation 4.

New Techniques in the Atomic Age

For 200 years it has been known that plants convert carbon dioxide of the air to carbohydrate. How they do it and through what types of intermediate compounds the carbon passes en route to sugar could not be determined until the advent of the atomic age. With labeled or radioactive carbon atoms it has been possible to find out which of the many compounds in plants are actually involved in the early stages of carbon-dioxide reduction. Such experiments involve substitution of radioactive carbon dioxide ($C^{14}O_2$) for ordinary carbon dioxide during the normal photosynthetic process. The plant then begins to lead the labeled carbon atoms through its series of reactions. If the plant is now rapidly killed by immersion in boiling alcohol, one obtains a solution of the radioactive compounds formed during such a short period. A method for observing these labeled compounds has been developed by the authors' laboratory and results in pictures such as that shown in figure 5. This is a radiogram or picture of the radioactive compounds formed by barley leaves during 5 minutes of photosynthesis. The many compounds in the plant are separated by movement of solvents in a large sheet of filter paper. By use of solvents in two directions, one obtains a characteristic pattern or map of compounds. Which of these is radioactive is demonstrated in the X-ray film which was exposed to the paper. By examining such radiograms much can be learned regarding the chemical functions of plants and the effects of environmental changes upon these functions.

Such investigations have led to a tentative theory regarding the series of chemical transformations by which carbon dioxide is reduced to organic compounds within the plant. This theory is depicted in abbreviated form in figure 6.

In this scheme, only the carbon atoms of the organic molecules are shown, and each arrow may represent one or many chemical steps. This schematic representation is necessary both for simplification and also because many of the actual intermediates and specific chemical steps are not yet known.

Starting with a two-carbon compound (A), it is thought that chemical addition of carbon dioxide results in a three-carbon compound (B). Part of the molecules of (B) thus formed add another carbon dioxide molecule to give a four-carbon compound (C), which is split to give two two-carbon compounds (D). The latter are transformed by the reducing

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power from the light (carried by the reduced compound RH_2) to give the starting compound (A), thus completing the cycle.

Some of the molecules of (B) are transformed to carbohydrate, while (B), (C), and (D) can all give rise to amino acids and hence to proteins through still another type of transformation. Finally, some of the two-carbon compounds, (A) or (D), may be used in the biological synthesis of fats.

The numerous transformations of photosynthesis are performed by enzymes which are specific proteins having functional groups and definite requirements for their action. The functional groups include many of the known vitamins, and the metal requirements include the known trace metals necessary for plant growth (such as zinc, manganese, copper, boron, etc.). As it becomes possible to study the action and requirements of these enzymes it becomes more reasonable to anticipate the external control of their activity within the plant. Thus, the efforts of a soybean plant might be directed toward the production of edible oils rather than protein synthesis by use of chemicals capable of blocking reactions necessary for protein synthesis, while at the same time requirements of the enzymes required for fat synthesis are satisfactorily met. In other cases, the yield of a particular crop may be enhanced by administration of a suitable chemical. Laboratory evidence already available is sufficient to indicate specific possibilities for field testing.

The continued investigation of new and improved plants will doubtlessly be productive of increased agricultural efficiencies. The study of an entirely different type of crop has been undertaken recently by various workers and may lead to a much more efficient utilization of light, water, and carbon dioxide than that obtained with conventional agricultural crops. This type of plant is the unicellular green algae which normally grow in vast amounts in the oceans, lakes, and ponds. Studies of growth conditions of these algae have shown that they can produce fats and proteins in much higher yields than can any of our cultivated crops. Whereas field crops (sugarcane, corn, potatoes, etc.) yield 5 to 15 tons per acre-year, experiments have shown that the green alga *Chlorella* can yield 30 to 100 tons per acre-year.

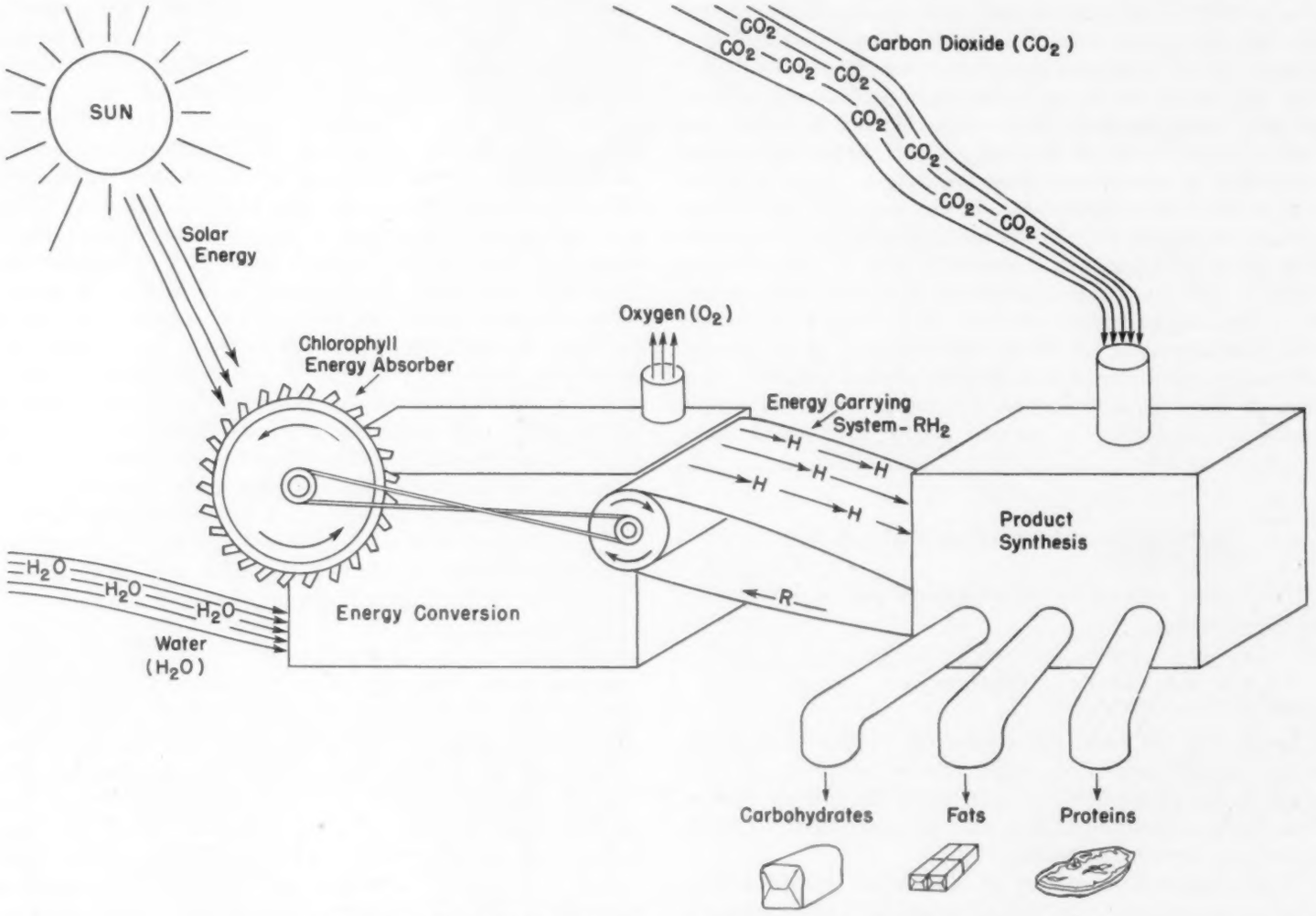

FIGURE 4.—*Photosynthesis—energy source, principal raw materials and products.*

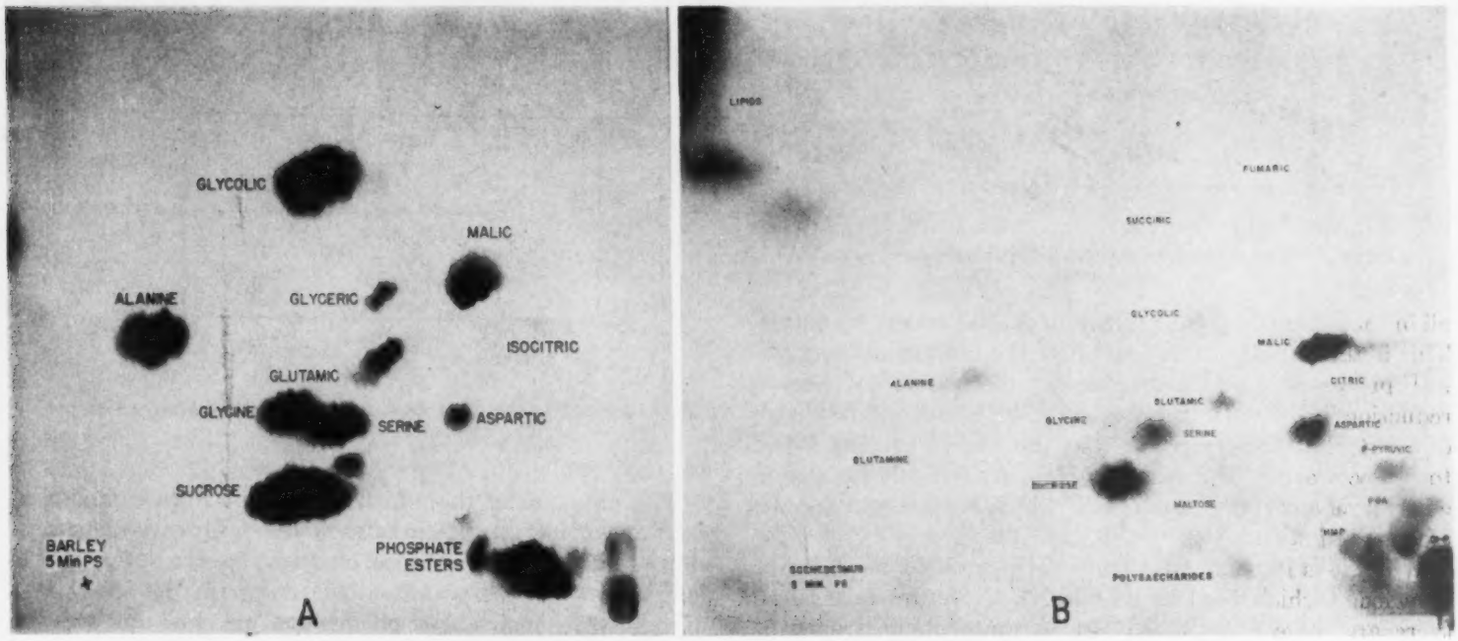

FIGURE 5.—*Chromatography—showing products after 5 minutes of photosynthesis—A. Barley leaves, B. Scenedesmus.*

Glycolic: $CH_2OH–COOH$
Malic: $COOH–CH_2–CHOH–COOH$
Glyceric: $CH_2OH–CHOH–COOH$
Citric: $COOH–CH_2–C(OH)(COOH)–CH_2–COOH$
} Common plant acids

Alanine: $CH_3–CHNH_2–COOH$
Glutamic: $COOH–CH_2–CH_2–CHNH_2–COOH$
Aspartic: $COOH–CH_2–CHNH_2–COOH$
Serine: $CH_2OH–CHNH_2–COOH$
Glycine: $CH_2NH_2–COOH$
} Common amino acids—constituents of protein

Sucrose: $C_{12}H_{22}O_{11}$ Commercial sugar

Phosphate esters: Compounds of the type $(CH_2O)_n–O–PO_3H_2$

The practical problems of growing and using such a crop are being rapidly solved. The economic and social value of such increased utilization of solar energy, particularly for countries like Japan and Israel, can scarcely be overestimated. The growing interest in such projects is evidence that it is now possible to consider seriously more efficient use of our photosynthetic potential.

Our knowledge of the mechanism of photosynthesis is scarcely commensurate with the importance to the welfare of the human race. The recent rapid progress in understanding this process has stimulated its application for increased human use of solar energy. It now seems reasonable to anticipate more efficient absorption and storage of this most abundant and valuable natural resource, solar energy.

One large source of materials and energy used by man is that obtained from coal, gas, and petroleum. These materials were derived from photosynthesis during a long period of geological time and are at present being used at a much more rapid rate than they are being laid down. Consequently, an increased direct utilization of solar energy will have to be found as these materials are exhausted. Since photosynthesis is our most efficient means of converting solar energy to fuels, we should begin to think of long-range plans for increasing the efficiency and utility of this conversion.

Of more immediate concern is the problem of increasing the yield of food for man from photosynthesis. Naturally, such a fundamental problem has attracted many investigators from a variety of fields, and a vast amount of research on this subject has been done during the past two centuries.

One type of research has been concerned with measuring the over-all scope of photosynthesis. This research results in such calculations as the gross amount of carbon reduced each year, a figure currently estimated at 10 billion tons. Figure 3 contains the results of some other calculations of this type.

A second type of research is concerned with improvement of soils and the use of nutrients. Such improvement goes back many centuries to the first use of fertilizers. Modern-day soil research is to some extent still empirical. For example, the requirements of trace elements such as tungsten, manganese, and zinc for proper plant growth have been determined empirically and are only now beginning to be understood.

A third type of research which has been very successful is the development of improved strains of plants. Investigations of optimum planting time, temperature zones, optimum times for irrigations, etc., have been productive of increased crop yields.

Another type of research, more fundamental than the above, may eventually result in the greatest improvement of

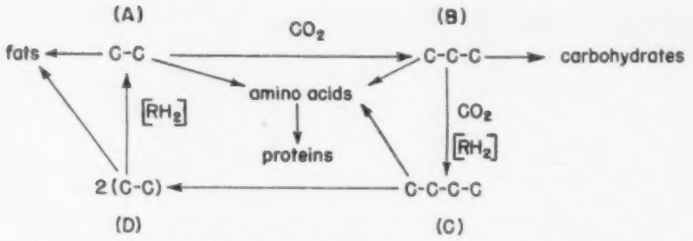

FIGURE 6.—*Transformations from carbon dioxide to complex carbon compounds.*

all in the efficiency of the utilization of solar energy by plants. This is the detailed investigation of the individual biochemical processes which comprise the mechanism of carbon reduction in plants. For example, an intimate knowledge of plant biochemistry shows that the trace elements, found to be necessary by the soil researches, are actually associated with specific enzymes, the agents which bring about specific biochemical steps.

While it is impossible to know or suggest all the areas of knowledge which need to be filled in by future researches, there are some areas which are in quite obvious need of immediate attention. First of all, we should know more about the mechanism of light absorption by the plant. This is called the photochemical step of photosynthesis. In this step, the plant's green pigment, chlorophyll, absorbs light energy and in some way converts this energy to chemical energy. The efficiency of this conversion has been studied extensively, but little is known about its mechanism. Under optimum conditions in the laboratory, efficiencies as high as 85 percent have been measured, but the efficiency is ordinarily much less. Increased knowledge of the chemical and physical processes involved in this step might well lead to increased efficiencies under agricultural conditions.

Also pertinent to the optimum utilization of solar energy for photosynthesis is a knowledge of the intensity of this energy over the earth's surface. The energy is, of course, dependent upon latitude and weather. A map of solar-energy intensity and its dependence upon the time of year at various points throughout the country would prove invaluable in determining which plants and growth condition could most efficiently utilize the available energy. The effect of industrial dust and smoke on light intensity and subsequently on agricultural yields should be evaluated. Existing and new weather-measuring facilities could be employed to supply more complete data regarding light intensity and total energy for such a survey of photosynthetic potential.

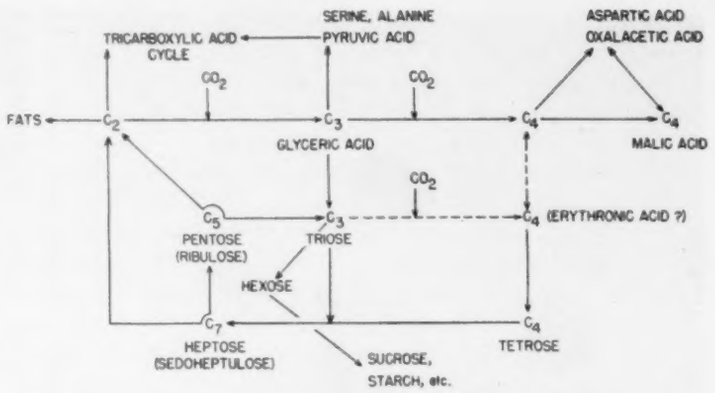

FIGURE 7.—*Sequence of chemical processes in photosynthesis.*

The direction of the efforts of a plant toward flowering, fruition, or leaf growth is often a response to the length of day and night. For instance, cherries flower in spring during long days while chrysanthemums flower in the short days of fall. Although these phenomena are well known, the reasons for them are not understood. Advancement of fundamental research to learn the mechanism of such response to short days may well result in our being able to control such responses by chemical treatment. It would be of great value to be able to hasten the flowering of wheat, beans, or rice and thus gain time for production of another crop on the same soil. It should be possible to disturb the delicate balance of photosynthetic products which give rise to flowering. An interesting example is found in sugarcane, which flowers, thus disturbing its productivity, when the days and nights are equally long. One minute of illumination at midnight during this period will prevent flowering and thereby result in an increase in sugar production. The possibility that chemical stimulation could give the same result is worthy of investigation.

The necessity for continuing and expanding these researches can hardly be overemphasized. The importance of water as a national resource is being increasingly realized. Carbon dioxide and solar energy, the other two photosynthetic ingredients, are also national resources, and should be so recognized. Only by increasing our knowledge of all aspects of the process by which these resources are utilized can we hope to improve the production of food, and eventually of fuel, to the extent which will be necessary to meet growing requirements.

The Sun's Radiant Energy in Photosynthesis and Its Position in Energy Resources[1]

By FARRINGTON DANIELS, *Professor of Chemistry, University of Wisconsin*

FROM THE DAWN of history man has realized the importance of the sun, but only in the present scientific age has he begun to appreciate the vastness of this source of energy and the extraordinarily clever mechanisms by which nature makes efficient use of it. In these times of profligate spending of the world's natural resources and uncontrolled increase in population we should consider the future and investigate what help we can obtain from science.

When we have used up our coal and oil, exploited our available land with intensive farming and trebled our population, can we then call on the sun to give us still more means to satisfy our ever-increasing demands for food, fuel, and power? The answer is "yes." But there is a long challenging road of research and development which must be followed first—and we must not get the idea that we are about to step into a new era of physical and economic abundance. We can't eat sunshine; we can't carry it where we want to use it; and, because it cannot easily be used to produce high temperatures, we find it is difficult to apply directly in our heat engines.

Amount of Solar Energy

How much energy does the earth get from the sun to use for food and fuel and power? One square foot of land in the United States receives on an average about 1 kilocalorie of heat per minute. This amount of energy will vary—from summer to winter and from Maine to Arizona—but that average is not far from 1 kilocalorie. One kilocalorie is about as much heat as is evolved in burning half of a wooden match.

Let us visualize solar energy on a larger scale, however. An acre of land contains somewhat more than 40,000 square feet and the sun shines, on the average, about 500 minutes per day. One kilocalorie when multiplied by the 40,000 square feet of an acre and by the 500 minutes of sunlight per day gives us a total of 20 million kilocalories of sunlight and heat per acre per day. How much of this heat are we entitled to? How many acres of land have we? Theoretically and statistically, each of us is allotted 14 acres. This is the value obtained by dividing the total land area of the continental United States, about 2 billion acres, by the number of people living in the United States, about 160 million. If all the land were divided equally among all the people, each of us would then be entitled to 14 acres, and to 14 times 20 million, or 280 million, kilocalories of solar energy per day.

How much energy do we need to maintain our present civilization? Here again we shall discuss the situation in the United States, for which data are available, rather than in the whole world. (Most of the data have been taken from the World Almanac for 1946.) Each of us consumes as food the equivalent of about 3,000 kilocalories. The amount of energy which we use as food is small, however, compared to the amount of energy used to run our machines and keep us warm. If one took all the coal and oil and gas produced in the United States in a year and divided it by the number of days in the year and by the number of people in the United States, one would arrive at the figure of 147,000 kilocalories of heat per day per person in the United States. These 147,000 kilocalories of fuel are used for heating houses, driving automobiles and trains, producing iron and steel in blast furnaces, generating electricity, and carrying out all our manufacturing processes.

The 147,000 added to the 3,000 for food gives us 150,000 kilocalories as the actual consumption of heat energy per person per day in the United States and we have just seen that theoretically each person is entitled to 280,000,000. This looks like a very large factor of safety; the daily supply is nearly 2,000 times as large as the daily requirement. But these figures are completely misleading. We cannot store sunlight as sunlight, and we cannot carry it around with us. When we get down to the cold facts of utilization of sunlight, we see that this margin of safety in solar energy is largely illusory. Certainly at the present time solar energy cannot compete on an economic basis with the products of solar energy stored up millions of years ago in the form of organisms and plants and preserved for our convenient present use as coal, oil, and gas.

Photochemical Utilization of Solar Energy

Solar engines are not economically practical as yet because the temperature produced by the sun is low and the capital investment in the machinery is high. And so we will consider here other possible ways of utilizing the sun's light. It would be a good idea to bring about some photochemical reaction

[1] Taken in large part from the American Scientist, 38, 531–548 (1950).

that would store up energy in new chemical compounds as a result of the action of sunlight. This photochemically produced material would be of such a nature that it could react in the reverse direction under suitable conditions or react with some other cheap material so as to give back a large fraction of the energy absorbed from the sun. Cheap and easily obtainable chemicals would be required for bringing about such a photochemical reaction. One would naturally think of carbon dioxide and water, and one can write as a chemical reaction:

$$H_2O + CO_2 + \text{light} = CH_2O + O_2$$

This chemical compound represented by CH_2O is a carbohydrate—$(CH_2O)_6$ is glucose—and it could be burnt in the oxygen of the air to give back CO_2 and H_2O with the release of a considerable amount of heat at a high temperature, suitable for operation of efficient engines.

This reaction would seem to offer good possibilities, but a theoretical study indicates practical difficulties because carbon dioxide and water are transparent to sunlight and unless light is absorbed no photochemical reaction is possible, and moreover the energy in a unit of sunlight is not great enough to bring about the reaction suggested here. If a carbohydrate is burned with air, 112 kilocalories are evolved by an amount of organic material which corresponds to one gram atom of carbon. To reverse the process would require at least 112 kilocalories per mole and probably more. But the energy of sunlight in the red region of the spectrum amounts to only 40 kilocalories. In the laboratory no one has yet succeeded in making several low-energy units of radiation (photons) combine to do a high-energy job. Nature, however, has been carrying on this reaction ever since life started on the earth. Nature combines CO_2 and H_2O into a carbohydrate by means of a series of steps, the process of photosynthesis, which we are just beginning to understand.

Although carbon dioxide and water are transparent to ordinary sunlight, the green chlorophyll found in most living plants absorbs very completely most of the visible sunlight, extending from 4,000 angstroms in the blue region to 6,500 angstroms in the red. It then transfers this energy of sunlight to the water and releases hydrogen, which in turn reacts with carbon dioxide or with its reduction products and produces a variety of complex intermediate compounds, including sugars and other carbohydrates, represented by the formula $(CH_2O)n$.

Chlorophyll is a unique and most remarkable substance. It has intense absorption bands in red and blue light. Absorption of green light is very much less, but in thick layers chlorophyll will absorb practically all the green light as well as the blue and red. So in forests or in agricultural fields where there are several layers of green leaves, most of the visible sunlight is absorbed by the chlorophyll of the plant, and it is all about equally effective in producing organic material. The red and blue light is absorbed nearest the surface, the green light deeper down. The same situation is found among green algae and aquatic plants in lakes and in the ocean.

In any study of this process of photosynthesis it is important to know the maximum efficiency possible. What fraction of light absorbed by chlorophyll in a living plant can be utilized in the production of organic materials? If one were to burn in air the plant material produced by photosynthesis and measure with a calorimeter the heat evolved, what fraction of the original heat absorbed from the sun would be returned?

Maximum Yields of Agricultural Crops

We have seen that an acre of land receives 20 million kilocalories of solar radiation per day. Half of this radiation is absorbable by chlorophyll. In the visual light range, then, a maximum of 3.65 billion kilocalories could theoretically be absorbed per acre per year in plant growth. If it were possible to grow agricultural crops on this acre of land throughout the year in such a way as to store up 20 percent of this solar energy, the greatest possible theoretical yield would be about 730 million kilocalories of stored energy. It would take approximately 200 tons of organic material to yield these 730 million kilocalories of heat when burned in air. Actually, the average corn crop amounts not to 200 tons per acre in the United States but only to about 2 tons of total organic material per acre, assuming a harvest of 33 bushels of corn per acre (the average in the United States for 1946) weighing 0.9 ton, with the roots, stalks, leaves, and the rest of the plant weighing another 0.9 ton or so.

At first glance this seems to be a very low return, but another look at the conditions involved indicates a fair degree of efficiency in the production of this organic material. First, we must observe that the growing season in the United States is only about 4 months, or one-third of the year. Our 20 percent maximum efficiency would drop then to 6.6 percent utilization of the total supply of solar energy. Also we must note that only about one-half of the energy received from the sun falls in the visible region of the spectrum and is absorbed by chlorophyll. The other half is in the form of infrared or heat radiation. This is not absorbed by chlorophyll and does not take part in ordinary plant growth. The 6.6 percent utilization, therefore, is reduced to 3.3 percent. On the basis of experimental measurements at the University of Wisconsin and at the majority of other laboratories in the United States, this 3.3 percent utilization of the solar energy would seem to be a maximum.

The 20 percent laboratory efficiency of the process of photosynthesis (equivalent to 3⅓ percent limiting efficiency on farms) was obtained under optimum conditions with plenty of water and an ample supply of fertilizer and trace elements of all kinds required in plant growth. Furthermore, the experiments were performed with optimum amounts of carbon dioxide (up to 5 percent), whereas the carbon dioxide content of the air over a farm is only four-hundredths of 1 percent. Most important of all, under field conditions the high intensity of light reduces the efficiency of the chlorophyll still further. The total amount of organic mate-

rial which can be produced from sunlight by growing plants increases with the intensity of light up to a certain point, but beyond that point the amount produced does not increase, and the amount produced per photon of sunlight decreases rapidly when the intensity of light increases. Light of high intensity apparently stimulates a process of photo-oxidation which partially offsets some of the photosynthesis. In the laboratory experiments which gave the maximum yields of 20 percent, the intensity of the light ranged from 4,000 to 20,000 ergs per second per square centimeter, whereas the intensity of absorbable sunlight on fields is of the order of 200,000 ergs per square centimeter per second (excluding the infrared) an intensity so great that if it were used in these laboratory experiments the efficiency would fall far below the 20 percent maximum.

It is clear then that the combination of high light intensity, low carbon dioxide content, and the possibility of inadequate moisture, fertilizer, and trace elements will combine to make the 3.3 percent utilization of the annual supply of sunlight an unobtainable theoretical limit. In present agricultural practice the production of corn averages 33 bushels per acre, which represents the storage of one-tenth of 1 percent of the annual supply of solar energy which falls on the acre. Actually this is not too bad a showing considering the limitations already discussed. However, on fertile fields with good sunlight, high temperatures, high moisture content, and generous application of fertilizers, hybrid corn has yielded at least 100 bushels of corn per acre. This 100-bushel crop would correspond to a utilization of about three-tenths of 1 percent. In Hawaii, sugar cane is grown the year around, and the conditions of moisture and good soil are unusually favorable, so that the yield of organic material has amounted to considerably more than the 0.3 percent.

These high yields of agricultural products are possible only where the soil and moisture conditions are unusually favorable. What about other areas of the world where the illumination by sunlight is just as good but the land is less suitable for successful agriculture? It has been shown that in northern Wisconsin the use of scientific forestry methods should make it possible to obtain 2 tons of dry organic material per acre per year from an aspen forest. Such a continuing production would involve waiting 10 years for the initial growth and then removing selected trees each year so as to maintain a continuing forest that absorbs most of the sunlight which falls on it. The two tons of material would include the branches and leaves and roots, as well as the trunks, so that the matter of harvesting all this organic material per acre would be an expensive operation. Very large tractor harvesting machines involving a minimum of labor would be required.

It is evident that 2 tons of organic material can be produced on an acre of land even when the land is not particularly suitable for conventional agricultural purposes. In Florida, with more favorable conventional agricultural conditions, about 3 tons of dry organic material can be obtained per year from a forest of pine trees.

An acre of a fresh-water lake will yield about 2 tons of dry organic material in the form of algae. Weeds and aquatic plants would give about the same amount of dry material per acre per year. As in the case of an average corn crop, the cheaper crops in forests and lakes enable one to store up about one-tenth of 1 percent of the annual supply of the sun's energy. Special grasses and bushes might well be developed for obtaining a maximum amount of organic material from prairie land in arid regions.

Researches on the Utilization of Solar Energy

Another approach to the production of fuel lies in the large-scale growth of aquatic organisms such as diatoms which, under certain conditions, produce a considerable amount of fats and oils. Long-range research with selection and breeding might lead to the production of liquid fuels when the world's petroleum and shale oil reserves approach exhaustion.

Attempts have been made to achieve the intensive culture of plants and vegetables without soil. This is the science of hydroponics. It has indeed been possible to produce unusually large crops per acre, using troughs of fertilized water or nutrient solutions in sand and thus eliminating the use of ordinary soil. Yields can be increased by this method, but the capital investment seems to be too large for present economic consideration except under special conditions such as the supplying of fresh vegetables to an Army base on a barren island in the Pacific.

Is there any chance of beating nature at her own game and developing artificial photosynthesis with organic dyes and enzyme substances? Might not these cause the combination of carbon dioxide and water using reactions somewhat different from those occurring in the growth of green plants? There seems to be no theoretical reason why such a development cannot be successful in the distant future. Possibly a combustible material could be made which is not reduced from carbon dioxide as far as cellulose or carbohydrate, and which would be easier to prepare because of the lower energy requirements. Up to the present time, however, no one has succeeded in combining carbon dioxide and water through the agency of sunlight in the absence of living cells.

Intensive long-range research should be continued along these lines, but it seems unlikely that within a predictable time such artificial photosynthesis could compete economically with ordinary growth. Chlorophyll is extremely abundant and does an extraordinarily efficient job of photosynthesis. One can hardly imagine producing any organic material which would be as cheap as the green leaves with which nature provides us. Furthermore, any practical application of photosynthesis on land would probably require large troughs containing the chemically reacting materials. It would cost at least $15,000 to cover an acre of land with a concrete trough and it would probably cost about as much more to cover the trough with glass. Obviously such a capital investment is prohibitive in comparison with farm land which can be purchased for prices ranging around $100

an acre. Plastic materials for troughs and covers offer intriguing possibilities for lowering the capital investments.

Cellulose present in hay, wood, and other plants cannot be used directly for human consumption but theoretically it can be used indirectly after being hydrolyzed with acids. It is possible thus to obtain carbohydrates which will supply energy for animals, which in turn can be used as food for animals and man. It is possible also to obtain proteins. These as well as carbohydrates are absolutely necessary for the continuation of normal life. Extensive researches have shown that it is possible to grow yeasts on a large scale, using carbohydrates which can be made from the hydrolysis of celluloses and other cheap organic material. These yeasts in turn can be grown so as to give a high percentage of protein. In fact, yeasts can give as high a percentage of protein as does beefsteak. It is reported that these protein yeasts have a sufficient variety of material to satisfy the nutritional needs of animals. This production of protein, through the growth of yeasts, has been practiced in the West Indies and could well be expanded on a large scale, particularly in the tropical areas where the production of meat through agriculture is difficult and expensive. There is still the matter of taste, but in view of the record of laboratory achievements in developing desired colors and smells it seems safe to predict that through sufficient research artificially produced food could be made to meet almost any desired requirements.

In many lakes and ocean bays, aquatic plants and algae could be used for food after suitable treatment, but the cost of harvesting is very great. Sometimes the algae are a nuisance, particularly when the lakes are fertilized with sewage affluent. Research should be undertaken in harvesting these algae and removing the odors and the fertilizing materials. Experience gained here could be used for harvesting aquatic food in the tropics. These algae are high in proteins and offer good promise for food after further research.

In some areas of the world an increase in the food supply might lead merely to an increase in the population, with no improvement in the standard of living of the people. However, when there is improvement in the scale of living, such as that which follows education and increased production through industrialization, the population increase often becomes normal and ceases to be a serious problem. An ample food and fuel supply is necessary for the creation and continuance of modern industrial development with higher standards of living. Food depends upon solar energy while fuel depends upon either solar or atomic energy.

Conclusions

In the foreseeable future it seems likely that atomic power will be utilized in large central stations involving heavy capital investments, and that solar power may well be employed in simpler decentralized units involving less expense.

Practical atomic and solar power will come slowly, but both have considerable promise. This promise can be realized only with the help of vigorous, sustained research programs. A research program for solar energy, such as has been outlined here, involves two types of research: fundamental pure research, and applied or developmental research. Both are important, but the latter cannot long continue without the former. The organized programmatic attack by teams of investigators, which proved to be so effective in the last war, is particularly successful in applied research. In normal times applied research for industry is frequently undertaken by private enterprise if there is a chance for financial returns. Particularly in the agricultural use of solar energy, applied research has been very successful in Federal and State experiment stations.

Fundamental research thrives best when individual scientists follow frontier paths which they themselves find and follow just for the fun of exploration and without having any particular goal in mind. Underlying principles are sought, together with correlating mathematical formulas and stimulating hypotheses which ever lead to new experiments, and on the way the scientists are always looking for new ideas and new techniques. This type of research flourishes in the universities, but private or government funds are also needed to encourage it.

Atomic energy for military purposes was developed with the aid of $2 billion in three war years under conditions of centralized authority and secrecy. It would be interesting to see what might be done with $2 billion in 3 years for the greater utilization of solar energy for peaceful purposes under conditions of decentralization and independent initiative, aided by rapid publication of results.

Summary

On an average day the sun gives 40 million kilocalories of light and heat to each acre of land in the United States. About half of this energy can be absorbed by chlorophyll, which is the green material of plants. If plants have a growing season of 4 months, absorb half the incident radiation, and cover the land completely, they can absorb a maximum of 2.4 billion kilocalories. However, under the most favorable conditions in the laboratory only 20 percent of this energy or 480 million kilocalories can be stored up in the form of organic material. Considering that the growing season is only one-third of the year and that only half of the sun's energy can be absorbed by the green chlorophyll, the maximum storage of energy in the form of carbohydrates and other organic material through the growth of plants is 3.3 percent of the annual supply of solar energy.

In agricultural plants the storage of energy is much less than this 3.3 percent because the sun is too bright and the carbon-dioxide content of the air is too low, and the optimum conditions of moisture, temperature, and complete fertilization cannot be maintained. A corn crop of 33 bushels per acre, which was the average in the United States for 1946,

gives about 2 tons of combustible organic material and stores about 0.1 percent of an acre's annual supply of sunshine. There are very few agricultural crops in the United States that yield more than 4 tons of dry organic material per year, and this weight corresponds to an energy storage of only 0.2 percent.

Some improvements in the utilization of sunlight can be brought about by further advances in agriculture, but very large increases in the utilization of solar energy will demand radically new approaches. Sunlight is as available on poor land as on good agricultural land, and intensive research may well show us how to make use of the sunlight which now falls uselessly on waste land or marginal land. This research could well be directed toward a better understanding of photosynthesis, toward engineering developments of inexpensive means of growing algae in tanks or transparent containers and harvesting them, and toward the direct storage of solar energy by chemical, physical, or electrical means.

Carbon Dioxide—The Principal Raw Material for Photosynthesis

By ELTON L. QUINN, *Professor of Chemistry, University of Utah*

THE FIRST written references to carbon dioxide suggest that even primitive peoples were aware of its presence. This important gas escapes from the earth in many places and can cause death to animals if inhaled. It was believed by the ancients to be an evil spirit or demon with the power to slay without leaving marks of violence on its victim. The material nature of the gas has been recognized at least since the time of Pliny, about A. D. 77.

The writings of van Helmont, who died in 1644, show a considerable increase in the knowledge of carbon dioxide; van Helmont not only recognized carbon dioxide as a gas distinct from other gaseous substances, but he was aware that it possessed special properties, many of which he studied. Besides the combustion of charcoal and fermentation, van Helmont found four other sources of *gas sylvestre:* first, by the action of an acid on carbonates; second, from caves, cellars, and mines; third, from mineral waters; and fourth, from the gastric fermentation in the intestines of animals. He was never able to collect and preserve carbon dioxide and even declared it could not be held in any vessel.

Joseph Priestley (1733–1804), whose fame is due largely to his discovery of oxygen, added much valuable information about carbon dioxide. The presence of a brewery near Priestley's home made possible a study of the gaseous products of fermentation. He found that plants were able to live in this gas whereas animals perished and, further, that plants under the influence of light used the gas and gave off oxygen and that this action ceased at nights.

Priestley's conclusions regarding the influence of living plants and living animals on the composition of the atmosphere have withstood the test of time. These ideas are even more remarkable when one considers that oxygen had not yet been discovered and the ideas regarding nitrogen were still vague. Priestley's conclusions can best be given in his own words:

> These proofs of a partial restoration of air by plants in a state of vegetation, though in a confined and unnatural situation, cannot but render it highly probable that the injury which is continually done to the atmosphere by the respiration of such a number of animals, and the putrefaction of such masses of both vegetable and animal matter, is, in part at least, repaired by the vegetable creation, and notwithstanding the prodigious mass of air that is corrputed daily by the abovementioned causes, yet if we consider the immense profusion of vegetables upon the face of the earth, growing in places suited to their powers, both inhaling and exhaling, it can hardly be thought but that it may be sufficient counterbalance to it and the remedy is adequate to the evil.

About this time Tobern Bergman formulated a statement on the composition of the atmosphere. He believed it consisted of three elastic fluids: first, acid of air (carbon dioxide) which exists in very small amounts; second, what he called vitiated air, which served neither for combustion nor for respiration of animals; and, third, an air absolutely necessary for fire and animal life, that makes up about a quarter of the atmosphere and which he regarded as pure air. While a great deal has been learned since the time of Bergman, the general over-all picture as he presented it has not changed much.

The part played by carbon dioxide in nature is of overwhelming importance. There is apparent chemical balance set up by nature between free and combined carbon dioxide, between animal and plant life, and between heat and chemical energy. In all these chemical reactions carbon dioxide plays an equal part with oxygen in spite of the fact that molecules of oxygen in the gaseous state outnumber the carbon-dioxide molecules 700 to 1. Many investigations have been made and much has been written in an attempt to explain how Nature maintains an equilibrium between these various reactions.

The life processes of both plants and animals revolve around the changing states of carbon dioxide. It is the principal raw material of the vegetable kingdom, and its regeneration occurs as a part of the most vital functions of all animal life.

Occurrence in the atmosphere.—The determinations of the amount of carbon dioxide in the atmosphere are of vital importance to the analyses of the process of photosynthesis. Widely different measurements have been secured by different investigators. Haldane, investigating the concentration of carbon dioxide in the country air near London, obtained values from 0.021 to 0.044 percent by volume. In the city air of London during still weather the values ranged from 0.0425 to 0.09. On the other hand, Carpenter, in this country, in reporting the results of over 1,000 analyses made in New Hampshire, Massachusetts, and Maryland, in spite of the widely different local conditions at the three laboratories, found no measurable differences in the atmospheric concentration of carbon dioxide between locations and seasons or because of proximity to large consumers of fuel. There has come to be, however, general agreement that 0.031 represents the volume percentage composition of average country air.

Assuming this average of 0.031 percent by volume (0.0474

percent by weight) for the atmosphere all over the earth, the total weight of this gas in the earth's atmosphere can be calculated. Taking the diameter of the earth as 12,742 kilometers, its area would be 510,110,000 square kilometers. The total weight of the atmosphere would then be 5.27×10^{18} kilograms (or 52,700 trillion kilograms). Using 0.0474 percent as an average the carbon-dioxide content of the atmosphere would weigh 2,750 billion short tons.

Occurrence in the hydrosphere.—Nearly three-quarters of the earth's surface is covered with water, in which various substances are dissolved or suspended. While the nature and amount of the dissolved materials may vary over a wide range, carbon dioxide is always present whether the solution be the brines of the oceans or the pure fresh water of a mountain lake. The dissolved carbon dioxide may be designated as "bound," "half-bound," or "free." The bound carbon dioxide is associated with calcium and magnesium, the half-bound exists in the form of bicarbonates, and the free carbon dioxide is in solution as a molecular substance. The free carbon dioxide is in equilibrium with carbonic acid and the ions resulting therefrom. Equilibrium conditions set up by ions in pure water are well understood, but there are many complicating factors in natural surface waters from biological reactions, sustained matter, and dissolved substances.

The waters of the earth act as great equalizing reservoirs which play an important part in keeping the carbon dioxide of the atmosphere at a nearly constant concentration. Complete equilibrium conditions may never actually exist between the carbon dioxide in the air and the water, but there is always a tendency toward such an equilibrium.

It has been determined that the dissociation pressure of the bicarbonates in sea water for temperatures from 18° to 21° C. is 0.0005 atmospheres, and falls off to zero at the temperature of freezing water. The carbon-dioxide tension of normal air is about 0.0003 atmospheres. The colder parts of the ocean, therefore, are constantly removing carbon dioxide from the atmosphere while the flow of carbon dioxide is from water to the atmosphere in the warmer parts of the ocean.

The sea is our largest reservoir of dissolved carbon dioxide. The carbon-dioxide concentration in sea water has been found to vary from 0.01 to 0.07 percent by volume, which is a far greater range of variation than in the atmosphere. The waters of the ocean are not so easily and uniformly mixed as the gases of the atmosphere.

Based on an average concentration of 0.05 percent, carbon dioxide in the oceans amounts to 66 trillion tons—from 20 to 30 times as much as in the atmosphere.

Much of this vast reserve of carbon dioxide is involved in processes in which its combination and association with other elements undergo change, and most of these transformations constitute successive stages in a cycle of combination, decomposition, and recombination. The carbon dioxide in water is derived from a number of sources: First, the atmosphere, although the amounts so supplied must be small compared to the quantities supplied from other sources; second, inflowing waters accumulate carbon dioxide from decomposing organic matter; third, the respiration of aquatic plants and animals and their decomposition; fourth, bicarbonates from inflowing subterranean waters.

The principal factors decreasing the carbon-dioxide reserve in the waters of the earth's surface are, first, photosynthesis of aquatic plants; second, carbonate-forming organisms utilizing calcium oxide, magnesium oxide, silicon oxide, and carbon dioxide; third, escape to atmosphere.

Occurrence in the lithosphere.—The many fissures and vents scattered over the earth's surface are constantly pouring gases into the earth's atmosphere. Carbon dioxide is found in all these gases in quantities varying from low concentrations to a practically pure substance. Scattered over the earth, innumerable vents, fissures, and wells bring carbon dioxide to the surface in the form of water solutions, oil solutions, gas mixtures of various types, and as a nearly pure compound. A few of these gas vents have become famous—for instance, the Dog Grotto near Naples, the Valley of Death in Java, the Stygian Caves in Yellowstone National Park, and the Laacher Lake in Germany.

Soils furnish carbon dioxide to the atmosphere in large but variable quantities. The amount of carbon-dioxide evolution is closely related to the density of the plant cover since this release of carbon dioxide is a reversal of the process of photosynthesis. Most of the carbon dioxide is evolved in the surface layer, chiefly by microflora.

In practically all cases, carbon dioxide as it comes from the earth is associated with water in quantities varying from a gas saturated with water vapor to water super saturated with gas. When the latter condition prevails, the acid character of the water dissolves considerable mineral matter from the rocks through which it flows, resulting in mineral springs. Many such springs are famous because of the curative properties of their waters, the beautiful and interesting formations from which they emerge, the force of their eruption, or other unique features.

Carbon dioxide balance in nature.—We can now go beyond Priestley's cautious statement that it was "highly probable" and say that it is certain that the injury done to the atmosphere by the respiration of animals and the putrefaction of both vegetable and animal matter is repaired by various chemical processes of which photosynthesis is the most important. There are no analytical data accurate enough to indicate whether there is progressive change in the carbon-dioxide concentration of the atmosphere. It is not unreasonable to assume that the rate at which carbon dioxide goes into the atmosphere and its rate of removal are approximately equal. In general, the factors which increase the carbon dioxide in the atmosphere are (1) the evolution of carbon dioxide from springs, gas wells, volcanic vents, etc.; (2) the combustion of wood, coal, petroleum, and natural gas; (3) the respiration of lower organisms, plants, and animals; (4) the decay of organic matter; (5) certain industrial processes—smelting of ores, lime burning and fermentation. The factors which remove carbon dioxide from the atmosphere are: (1) Photosynthesis by plants, (2) the formation of carbonates by organisms, (3) chemosynthesis by bacteria, (4) the weathering of rocks.

Factors increasing carbon dioxide in the atmosphere.—The respiration of animals is adding carbon dioxide to the atmosphere in great quantities. A human being expires, on the average, about 900 grams of carbon dioxide daily. On the basis of 2,000 million people on the earth, respiration alone would add 725 million tons of carbon dioxide to the atmosphere each year. This is approximately the same amount produced by burning 280 million tons of coal. There seems to be no way to make a convincing estimate of the carbon dioxide produced by animals other than human beings. However, most of the products of photosynthesis are consumed by the plants themselves or undergo decomposition into their original constituent elements, chiefly carbon dioxide and water. Probably a more staisfactory way of estimating the regeneration of carbon dioxide is to use the estimates for the annual products of photosynthesis, since in a general way it can be assumed that there is an approximate balance between the annual products of photosynthesis and the consumption of these products in processes which involve their decomposition.

The yearly consumption of coal in its various forms over the whole earth is approximately 2,000 million tons. The yearly production of carbon dioxide from this source would therefore be 5,126 millions tons (assuming 70 percent carbon).

Petroleum is next in importance as a fuel and a source of carbon dioxide. The world's annual production of crude petroleum is approximately 3,000 millions barrel of 42 gallons each. Assuming an average density of 0.9, the carbon dioxide produced from this source would be 1,466 million tons.

The annual consumption of natural gas in the United States is approximately 5 trillion cubic feet. Assuming that this gas averaged 95 percent methane, the carbon dioxide produced by complete combustion would be approximately 300 million tons. No data are available on the consumption of natural gas by other countries. Assuming that its use is approximately one-half as extensive as the use of petroleum, the ratio which prevails in the United States, the annual amount of carbon dioxide which enters the atmosphere from the combustion of this fuel would be approximately 650 million tons.

Plant Anatomy in Relation to Water Environment

By GEORGE J. PEIRCE, *Professor of Botany, Emeritus, Stanford University*

THE BODY of the higher land plants consists of tissues among which the various functions are divided and by which the various needs are met; but, while there is division of labor, each tissue and each organ of the plant may perform secondary functions, or be the seat of subsidiary phenomena. Thus the green leaf, primarily for the production of food, is the seat of maximum gas exchange and of water loss. The green leaf represents in its shape, size, distribution, anatomy, duration, and even number, the adjustment which each individual leaf, as well as the whole plant, makes among these and many other less evident phenomena.

Similarly the root, primarily for the mechanical support of the plant and the intake of water, must provide also for passing the water on to other parts of the body. But obviously these tasks vary according to diverse or changing external conditions, the intake of water from moist soil in the rainy season appearing to be easier and more understandable than by the same root from the same soil in the dry season. The facile statements that water intake by roots is an osmotic phenomenon, or that "work is done," ignore the fact that under conditions very different from those of well-watered areas the relative densities of the solutions in root and in soil are also very different.

Systems of Water Movement

In order to provide the path of water movement from soil to air through the body of the plant there must be a vascular system, again so flexible that it will meet the need of the plant in all of its circumstances, ranging from saturated soil and air to soil and air almost dry. Combining mechanical support and water lift, one finds the vascular tissues variously strengthened and the vascular tissues themselves variously composed of elements as different as the small one-celled tracheids of the wood of the conifers and the large many-celled vessels of the annual herbaceous plants of the rainy season. Furthermore, the same individual plant may regularly produce different conducting tissue in the same year according to the external environment.

Perennial land plants must survive these changes or succumb, either locally or extensively. Many annual plants cannot maintain themselves when the procession of the seasons from wet to dry entails these changes in the quantity and the state of the water within their conducting systems. Examination reveals that their vascular anatomy does not meet the requirements of adequate water holding and water lifting.

Between the so-called water reservoirs, which are cells and tissues evidently enlarged and otherwise fitted for containing water in their vacuoles, and the wet walls which not merely contain but actually hold water with great tenacity, there are many intermediates, differing from one another as do the environments in which the plants live. These wet walls vary in thickness as they do in hardness and stiffness. They may look as if they were mechanically strong where little or no mechanical strain can develop; but they may show by their chemical composition that they fix—adsorb and incorporate—water, perhaps in the manner in which the water of crystallization is incorporated in blue copper sulfate. It is recognized that the crystalline form and the crystalline state of copper sulfate depend upon the two constituents of the crystals, water and copper sulfate.

Similarly, but to a certain point only, and also only partially, the shape and the thickness of cell walls depend both on the chemical composition (cellulose derivatives and their accompaniments) of the cell wall and water. Collenchyma tissues, which are mechanically weak though looking as if they might have tensile or compressive resistance, do store amounts of water which are large in proportion to the mass. The amount of heat required to drive off all of this water indicates the force with which this water is bound; and the shrinkage shows no less plainly how much the form depends upon the constituent water.

Structure of Plants and Water-Carrying Capacity

In all of the plants thus cited, as well as in all the rest, the anatomical structure of the stems may be considered to be hereditary; but while the plants may vary according to circumstances, the limits of variation, as well as their behavior otherwise, seem to be set by hereditary characters, and we find the sweet pea failing to grow indefinitely in height in spite of the mechanical support of frame or trellis. The reason seems to be that the water-carrying capacity of its vascular system is limited.

The wood of the conifers, as is well known, is composed mainly of tracheids which, in proportion to their diameters, have thick walls. In these thick walls much water is tenaciously held. The majority of conifers are also evergreen, retaining their leaves for two or more years. Those which

are not evergreen live where there is ample moisture in soil and air. The evergreen conifers are distributed from well-watered to desert areas. Their monotonous wood anatomy enables them to meet this great range of circumstances. The vascular systems of the conifers, all built upon the same general plan, are equal to the great variety of conditions under which different species and individuals live. But the vascular systems are associated with leaves of limited area, limited water loss, and even limited number. The vascular systems can carry enough water to supply the leaves at all seasons. Only in the severest of dry seasons, in years of light winter snowfall and of rainless summers, does one see signs of suffering from lack of water. In such seasons the plants absorb what water they can from dry soil; they lose what they must from leaves restricted in area and in number, and may lose many needles during such summers; they make limited growth in length or may even die back extensively. In spite of the superiority of their vascular systems, one finds the desert pines as scattered individuals, not as close stands of forest or even chaparral.

In the mass of wet wood which constitutes a part of the vascular system of a living land plant, water may exist exclusively in liquid form, or part of it in liquid form, part of it as vapor. The liquid water may fill a duct or a tracheid, it may be "bound" in the walls, it may be more or less free on the surface of the walls as a thicker or thinner film, and it may fill as vapor the remainder of the space surrounded by the wet wall.

The proportions of hydrostatic to pneumatic tissues in the vascular system (of trees) vary from time to time according to the internal and external circumstances, there being very little if any pneumatic tissue at the time when bleeding is a natural or induced phenomenon, and very little if any hydrostatic tissue containing water other than as vapor, film, and bound water at times of deficit, when bleeding is not possible. The elements filled with water are obviously most numerous at times of water surplus, fewest at times of water deficit. The same set of ducts or tracheids will, therefore, be a part of the hydrostatic system at one time and of the pneumatic system at another.

Instead of the water being at all times in a larger or smaller number of unbroken columns of liquid, it may be in unbroken liquid columns or in hollow liquid columns (films on the walls) filled with water vapor, and water bound in the cellulose and cellulose derivatives of the walls.

Mechanism of Water Movement

These are the conditions of water movement in woody plants in arid and semiarid areas, and in all vascular plants at times of water deficit in the vascular tissues, whatever may be the condition at times of water surplus in humid climates whether tropical or temperate. That there may be great force (suction force) exerted by the foliar parts above upon the conducting vascular tissues below is obvious. Evaporation and transpiration from the surfaces, wherever they may be, will set up in the mass forces, tensions which will conform in place and power to the structure and composition of the system. The bound water of the walls of the vascular elements forms a water seal which obviates and excludes drawing in air from the sides. Hence the traction is upward, not lateral; it is a lifting force pulling up the water as vapor or as liquid, according to position and condition in the vascular system. That this force is adequate has been shown repeatedly.

The maintenance of water as vapor, liquid film, and liquid mass in the vascular elements and their walls, in the hydrostatic-pneumatic system of woody plants, is possible only when living cells are duly associated with the vascular tissues. Death of these cells by poisons and by heat, immediately interfering with the moving mass of water only to a partial extent, disturbs the movement of sap far less than cold, which completely stops the movement of the water as well as the life of the cells in the zone of freezing. The living cells are indispensable, not for moving, but for conditioning the movement of the water.

And any removal, by evaporation, transpiration, or otherwise, of any water from the mass so disturbs the whole equilibrium of the mass of water, supported everywhere by elastic cell walls, that water moves to the losing part, slipping along the surface of the elongated members of the vascular system, slipping along the inner surfaces of tracheids and ducts as swiftly as the stream of molecules of water is lost by transpiration from the leaves, provided that transpiration is not too swift for the maintenance of a sufficient film of water on the inner surfaces of the ducts and tracheids. Within these hollow cylinders of water there is water vapor, the freedom, amplitude, and speed of movement of which are greater than those of liquid water; but the constituent molecules of which, as they move more or less swiftly up a tree, may become alternately parts of liquid, parts of vaporous water, remaining always parts of the continuous wet mass of the tree until they fly off into the air.

A study of vascular anatomy, supplemented by experiment and otherwise, shows that the maintenance of a moving or movable film of water on the inner surface of a duct or tracheid depends upon the quantity of water in reserve in the wall; the thicker the wet wall in proportion to the diameter of the member, the more certain the movement of water. The size and proportions of ducts and tracheids, among other things, determine the heights which herbs, shrubs, and trees attain, and they do this because they determine the volume and speed of water movement. And since each duct and each tracheid, and each living cell, is a unit, although a constituent unit of the whole system of a living land plant, the amount, proportion, and speed of movement of water in one part may be quite different from the amount, proportion, and speed of movement in any other part, however close or however distant.

The amount of precipitation and the anatomy of the plants living in a given area are two of the chief factors which determine the character of the vegetation, limiting a natural area to desert plants, grass, chaparral, or forest, and correspond-

ingly limiting what man can do in the area. Attempts to establish forest, without irrigation and other care, in regions of limited rainfall and naturally supporting only grass or even chaparral, seem unlikely to succeed because the water-carrying capacity of the wood is unequal to the need of moving water fast enough from the roots in dry soil to leaves in dry air at any but limited heights above the ground. The height to which a plant can grow is the height to which its vascular system can carry water. This is determined by its wood anatomy—which is inherited—and by its environments. The relation of the anatomy to water is the dominant factor in the complex which is the living thing.

Water in Relation to Plant Growth

By PAUL J. KRAMER, *Professor of Botany, Duke University*

THE SUCCESSFUL GROWTH of plants requires light, suitable temperatures, an adequate supply of the essential nutrient elements, and an abundance of water. Light is seldom limiting to plant growth. During the growing season, temperature becomes limiting only at high altitudes and in the far north. Most soils contain sufficient of the essential nutrient elements for the growth of a variety of plants and any deficiencies for the maximum growth of crop plants are easily supplied by the application of fertilizer.

Over large areas of the earth's surface, however, plant growth is severely limited by the lack of water. This is reflected in the development of natural vegetation which consists chiefly of forests in the best-watered areas, grasslands where rainfall is deficient or uncertain during the growing season, and areas of very limited rainfall which bear so little vegetation that we call them deserts.

Every farmer and gardener knows that the successful growth of crops depends on maintenance of an adequate supply of soil moisture. Most of us have observed that even a short summer drought injures our lawns and reduces the yield of our gardens. The objective of this article is to show why water is so important to plants and why even a temporary deficit will greatly reduce plant growth and crop yields. This can best be done by first explaining the uses of water in plants and the soil factors which limit its availability, after which we will consider the specific effects of water deficits on plant growth.

Uses of Water in Plants

The important uses of water in plants can be classified under the following headings:

1. As a constituent of the living protoplasm.
2. In the maintenance of turgidity of the cells.
3. As a reagent in chemical reactions.
4. As a solvent in which food and minerals are translocated.

Water is the chief constituent of growing plants. Even a growing tree consists of at least 50 percent water, while leaves of such plants as cabbage or lettuce contain over 80 percent and the growing tips of roots and stems contain over 90 percent. In most plants, reduction of water content is accompanied by decrease in or cessation of growth, and excessive dehydration causes the death of most plants. Although a few plants and some seeds survive indefinitely in an air-dry condition they will not grow until their moisture content is increased. Only those cells which are completely filled with water or which are in a turgid condition supported by a high water content, will function normally. When the water content of plant tissues decreases only a few percent, the cells lose their turgidity and wilting occurs, accompanied by cessation of growth and interference with various physiological processes. Water also is an essential reagent in such processes as photosynthesis and the digestion of stored foods into simpler, soluble compounds. It serves as the solvent in which food and minerals move from place to place in the plant. All substances enter and leave cells in water solution.

Essential as are all these uses of water by plants the actual quantity consumed by them is relatively small compared with that required to replace the water lost in transpiration. Since growing plant tissue is essentially saturated with water and the air surrounding plants is usually relatively dry, large quantities of water evaporate from them, a process called transpiration.

Plants have been observed to lose twice their own weight of water per day during periods of hot, dry weather which favors high rates of transpiration. Studies made at Manhattan, Kans., showed that the average corn plant required only 2.2 quarts of water to provide for all the internal uses of water during the entire growing season, but actually absorbed a total of 54 gallons. Thus only about 1 percent of all the water absorbed by a Kansas corn plant is used in it and the other 99 percent evaporates from its leaves in the process of transpiration. While the relative proportions used in the plant and lost by transpiration vary considerably with different crops and climatic conditions, by far the larger portion is always used in replacing water lost in transpiration. The transpiration losses of several species are shown in table 1.

TABLE 1.—*Water lost in transpiration during the growing season by plants of various species at Manhattan, Kans.*

Plant and length of season	*Water loss in gallons*
Corn, May 5 to Sept. 8	54
Cowpea, May 19 to Sept. 2	13
Potato, Apr. 18 to July 30	25
Sunflower, May 26 to Aug. 23	123
Tomato, May 19 to Sept. 2	34
Winter wheat, Oct. 15 to June 28	25

Source: Miller, E. C., Plant Physiology, 2d ed., 1938.

The Amount of Water Used by Plants

Various methods have been used to express the amount of water used in growing a crop. The best known and probably the most useful value is the water requirement or transpiration ratio. This is the ratio of water used to dry matter produced by a plant during a growing season, or specifically the pounds of water used to produce a pound of dry plant material. There are wide differences between crops with respect to the amount of water used and there are considerable differences from year to year for a given crop. For example, in a series of experiments at Akron, Colo., the transpiration ratio varied from 1,068 for alfalfa to 287 for millet in a certain year, but the next year it was only 657 for alfalfa and 187 for millet (table 2). In general, millet, sorghum, and corn used the least water per pound of dry matter produced. Barley, wheat, oats, and rye used about twice as much, and legumes three times as much water as millet and sorghum. A native desert plant, franseria, used five times as much water as millet.

TABLE 2.—*Transpiration ratio or pounds of water required to produce a pound of dry matter at Akron, Colo.*

Plant	1911	1912	1913	1914	1915
Alfalfa	1,068	657	834	890	695
Oats	639	449	617	615	445
Barley	527	443	513	501	404
Wheat	468	394	496	518	405
Corn	368	280	399	368	253
Sorghum	298	239	298	284	303
Millet	287	187	286	295	202

Source: Data of Shantz & Piemeisal, Jour. Agr. Res. 34: 1093. 1927, as summarized in Miller.

Another method of expressing the amount of water required to grow a crop is in acre-inches. For example, if a single Kansas corn plant uses 54 gallons of water during the growing season, it may be shown that an acre of corn, under the same conditions would use the equivalent of 11 acre-inches of water to replace transpiration losses alone. In a recent study in Illinois a field of corn used 8.2 inches of water from June 1 to September 15, to replace transpirational losses (table 3). In the southern Appalachians a hardwood forest uses 17 to 22 inches of water annually, while comparable transpiration losses in a coniferous forest in the Sierra Nevada Mountains were estimated as the equivalent of 8 inches of water. This is actually only a portion of the water required to grow a crop, because in addition to the losses by transpiration, much water is evaporated from the soil and considerable is intercepted by the foliage and evaporates before it reaches the ground. These losses are sometimes combined and termed "evapotranspiration." Examples of what becomes of the water in certain areas are shown in table 3.

TABLE 3.—*Water usage by various types of plant cover*

Vegetation type	Corn (Illinois), June 1–Sept. 15	Hardwood forest (southern Appalachians), 1 year	Forest (Sierra Nevada), 1 year
	Inches	*Inches*	*Inches*
Precipitation	10. 1	62. 4	43. 0
Interception	2. 0	6. 4	6. 0
Evaporation from soil	5. 3	15. 1	3. 0
Transpiration	8. 2	19. 0	8. 0
Runoff	0. 0	19. 3	26. 0
Total loss	15. 5	59. 8	43. 0

Differences between precipitation and total water loss represent changes in stored soil moisture. Thus the soil under the corn crop lost 5.3 inches during the growing season, but the soil under the hardwood forest gained 2.6 inches in this particular year.

Compiled from various sources.

Availability of Soil Moisture to Plants

The soil can be regarded as a reservoir in which water from rainfall and irrigation is stored and from which it is removed by runoff, evaporation, and absorption by transpiring plants. The space available for water storage consists of the pores between the soil particles and comprises approximately 50 percent of the total soil volume. In a soil saturated with water by rain or irrigation, the pore space is completely filled with water, but within a few hours to a few days, gravity causes the water in the larger pores to drain away. This fraction of the soil moisture which moves freely under the influence of gravity is termed "gravitational water." It is of little direct use to plants because it usually drains away immediately, but if drainage is slow, it may be detrimental to plants because it interferes with root aeration.

After the gravitational water has drained away, the soil is said to be at its "field capacity." The water remaining is held in films around the soil particles and in the smaller pores, and is termed capillary water. It is this fraction of the soil moisture which is available to the roots of the plants. In soil permeated by roots of transpiring plants the moisture content is reduced gradually until absorption becomes so slow that the plants wilt. The soil is then said to be at its permanent wilting percentage, and the water remaining is held so firmly by the surfaces of the soil particles that it is unavailable to the plants. The water remaining in air-dry soil is termed "hygroscopic water," but as it is also unavailable to plants it will not be discussed. The relations of these various types of soil water are shown graphically in figure 8.

The field capacity and the permanent wilting percentage are particularly important values because they indicate the upper and the lower limits of that fraction of the soil moisture which is readily available for plant growth. The amount of

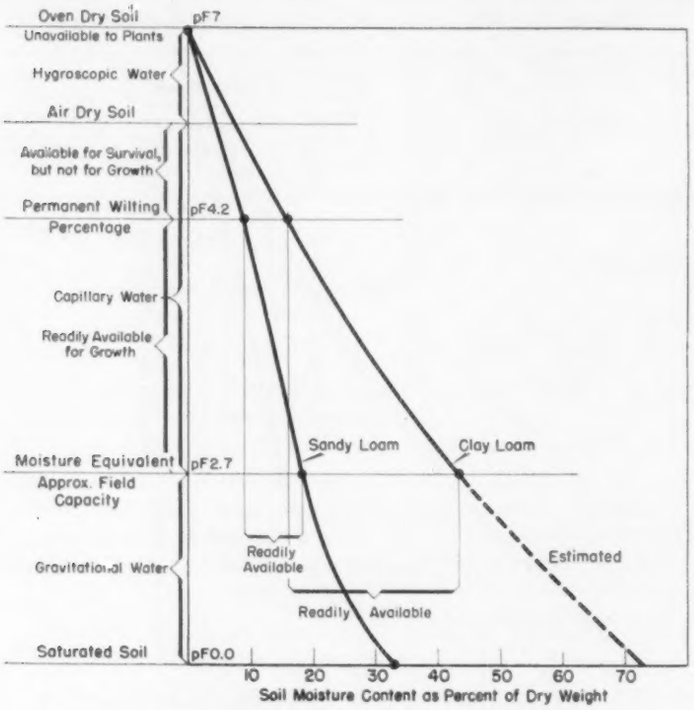

FIGURE 8.—*Relative availability of water in sandy and clay loam.*

available water varies widely in soils of different texture, generally being low in sandy soils and high in clays. This is because clay soils are composed of very small particles which possess a larger surface on which water can be held than do the coarser textured sandy soils. Moisture content is usually expressed as a percentage of oven dry weight, but soil moisture percentages have little meaning with respect to plant growth unless the field capacity and the permanent wilting percentage are also known. The amount of readily available water stored in several different soils is shown in table 4. Obviously plants growing in a soil such as the Oakley fine

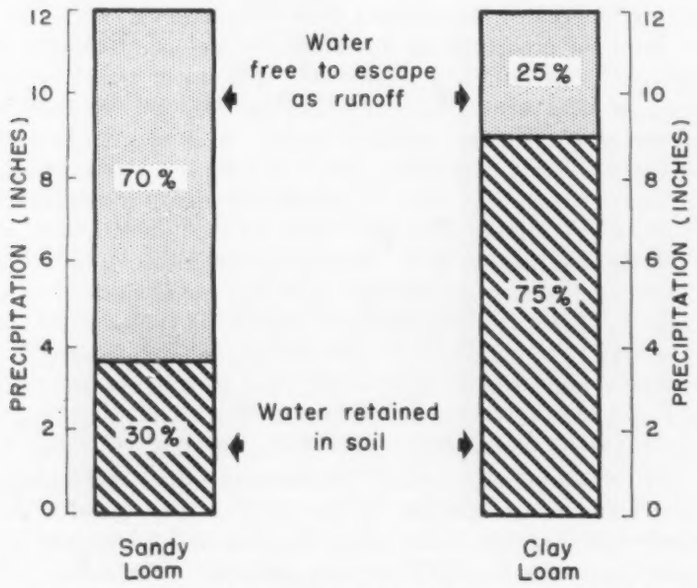

FIGURE 9.—*Relative proportions of rainfall retained in two soils.*

TABLE 4.—*Storage capacity of various soils for readily available water*

Soil type	Approximate field capacity	Permanent wilting percentage	Inches of available water per foot of depth
Oakley fine sand	3. 29	1. 33	0. 34
Yolo fine sandy loam	16. 80	8. 93	1. 26
Brockton clay loam	24. 50	11. 55	1. 98
Salinas clay	34. 50	16. 80	2. 83
Catherine loam	37. 90	19. 03	3. 08

sand with a storage capacity of only 0.34 inch per foot will suffer from drought much sooner than plants in a soil with a high storage capacity, such as the clays with 2.5 to 3.0 inches of available water per foot of depth (figure 9). In general, sandy soils must be rewetted by rain or irrigation much more frequently than clay soils if they are to produce good crops.

As the soil moisture content decreases below field capacity the films of water in the soil become thinner and the force or tension with which the water is held increases. This force is only one-third atmosphere or less at field capacity, but it increases until, at about 15 atmospheres, movement of water

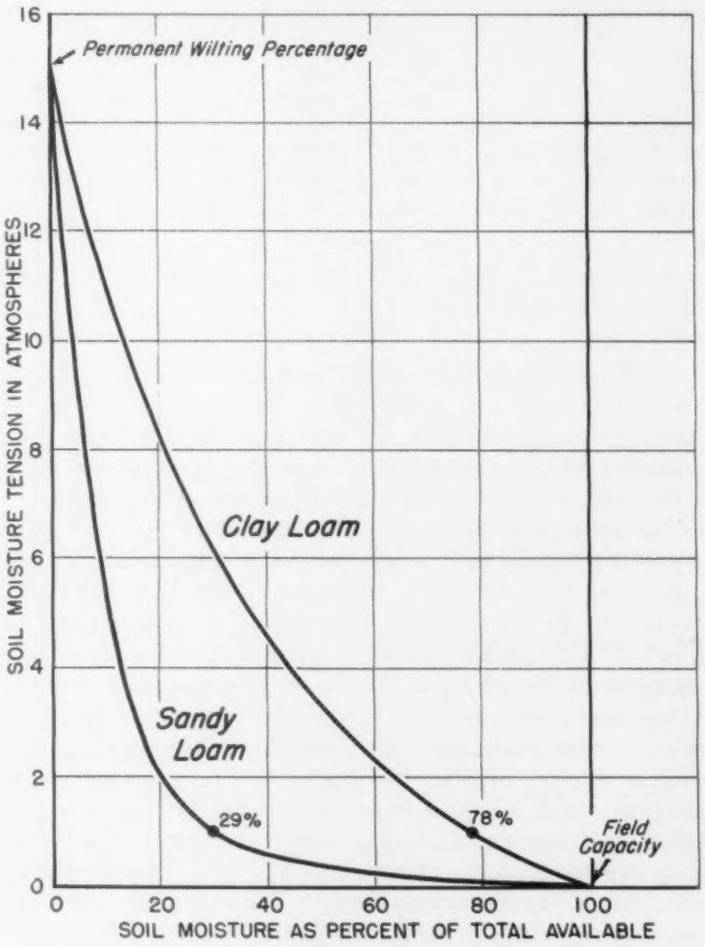

FIGURE 10.—*Soil moisture—tension and moisture content.*

into the roots becomes so slow that permanent wilting occurs. Figure 10 shows the moisture tension curves for two dissimilar soils. In the sandy soil most of the water is held with a tension of less than 1 atmosphere, but in the clay soil most of it is held with a tension much in excess of 1 atmosphere. In the latter type soil, moisture begins to limit plant growth before the permanent wilting percentage is reached.

In the more arid sections of the country the salt content of the soil often becomes so high that it limits plant growth. The water used in irrigation often contains 1 to 10 tons of salt per acre per year, and unless good drainage is provided, much of this salt accumulates in the soil. The most productive soils have an osmotic pressure of the soil solution at permanent wilting of less than 2 atmospheres. Some soils with osmotic pressures of 2 to 4 atmospheres produce satisfactory crops of alfalfa, cotton, sugar beets, and even wheat, but usually an osmotic pressure of 4 atmospheres or more seriously reduces yields of even salt tolerant species. While some salts probably are more toxic than others the chief effect is through reduction of water absorption and the resulting internal water stress produced in the plants.

Low soil temperatures also reduce water absorption, but this is seldom an important factor in the growth of crop plants, though it sometimes is important in greenhouses in the winter. Poor aeration also interferes with water absorption, but its effects are complex and largely beyond the scope of this article.

How Water Deficit Reduces Plant Growth

Lack of water not only reduces the quantity of plant growth, but also changes the quality. The most conspicuous effect of lack of water is reduction in size, but increase in amount of woody tissue is almost equally characteristic. Water deficit has multiple effects on plant growth because it not only affects the growth process itself, but also affects a number of different physiological processes which in turn affect the quality and quantity of growth.

It is easy to understand the direct effect of water deficit on the size of plants when we consider the role of water in growth. Continued growth involves the formation of new cells by cell division, the enlargement of these cells to many times their original volume, and their differentiation into various tissues of the plant. Lack of water interferes with all of these processes, but cell enlargement is particularly dependent on maintenance of a high moisture content. Increase in size of growing cells seems to be caused largely by turgor pressure produced by the diffusion of water into them. Whenever a water deficit develops in plant tissue, either because of excessive transpiration or slow absorption, the cells lose their turgidity and cease to enlarge.

That occurrence of internal water deficit causes stoppage or at least reduction of vegetative growth is corroborated by numerous observations in the field and laboratory. Growth of corn, asparagus, bindweed, and castor bean, for example, increases during the forenoon as the temperature increases, but is often checked toward noon by water deficits resulting from rapid midday transpiration. Bamboo, date palms, pine trees, and many herbaceous species have been observed to grow more during the night than during the day when the days are hot and dry and transpiration is rapid. Occasionally, if midday water deficits are particularly severe, growth may cease entirely and shrinkage of stems may even occur. The shrinkage of tree trunks and of fruits which has been observed during periods of high transpiration and limited soil moisture is caused by decreased water content of cells which are already largely matured rather than by cessation of growth.

Another kind of evidence of the importance of an abundant water supply is the relation of plant growth to soil moisture content. The growth of corn for example, has been found to increase with increasing soil moisture almost up to saturation, where soil aeration becomes limiting to the root systems. Growth of corn and potatoes is reduced by decreasing soil moisture long before the permanent wilting percentage is reached and corn plants subjected to repeated daily temporary wilting makes little or no growth. Sunflower plants, which are usually considered to be relatively drought-resistant, also show reduction in rate of growth before soil moisture reaches the permanent wilting percentage. Greenhouse and field experiments in recent years indicate that the yield of many crops can be materially increased by applying more water than was formerly thought necessary or even desirable. Such increases are only obtained, however, if all other conditions are favorable, and especially if an adequate supply of nitrogen is available.

Experiments conducted at the United States Regional Salinity Laboratory, Riverside, Calif., are particularly helpful in explaining the relation between soil moisture and plant growth. As previously stated, when soil moisture content decreases much below field capacity, the force or tension with which it is held begins to increase rapidly. Plants growing in the soil must absorb water against this force, hence they are also subjected to an increasing moisture stress which is equal in magnitude to the soil moisture tension. The relation between soil moisture content and moisture stress is shown graphically in figure 10 for a loam soil in which guayule was growing. As moisture was removed by the plant the moisture stress to which the plant was subjected increased slowly at first, and then very rapidly as the wilting point of the soil was approached. As shown in figure 11, an average moisture stress of only 4 atmospheres reduces the growth of guayule about 25 percent. Other experiments, the results of which are shown in figure 12, indicate that a moisture stress of 4 atmospheres reduces the growth of kidney beans over 50 percent.

The results of these and other experiments indicate that reduction in vegetation growth can be related mathematically to the average moisture stress to which the plant is subjected during the growing season. Since the moisture stress to which plants are subjected at permanent wilting approximates 15 atmospheres it is obvious that even short periods of wilting will result in average moisture stresses during

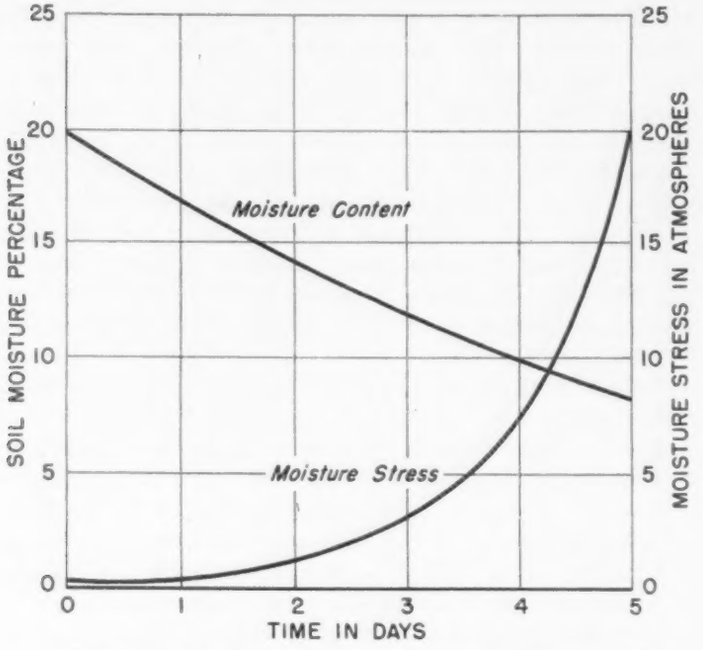

FIGURE 11.—*Relation of soil moisture stress and moisture content.*

the growing season high enough to seriously decrease growth. Only when plants are grown in soil kept wetted nearly to field capacity can maximum growth be expected. Over most of the United States, periods occur every summer during which soil moisture is sufficiently limiting to most crops that increases in yield might be obtained by irrigation. Knowledge of the range of soil moisture stresses to which plants are subjected during their growth would be much more useful than rainfall data in evaluating the relation of moisture to growth.

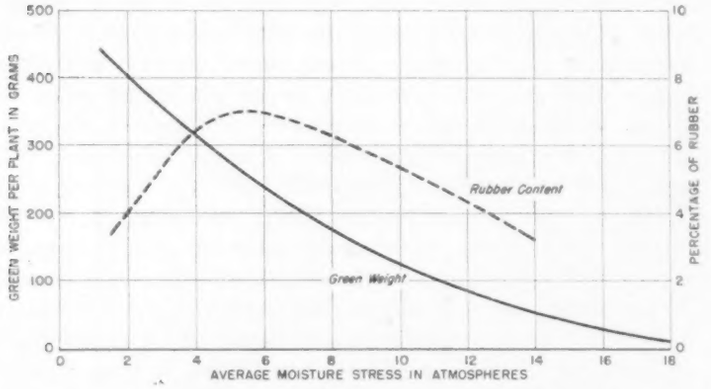

FIGURE 12.—*Effect of moisture stress and vegetative growth.*

Indirect Effects of Water Deficits

Deficient moisture supply produces various indirect effects on plant growth, a few of which will be mentioned. Photosynthesis usually is greatly reduced as the moisture content of leaves decreases. This reduction is attributable in part to decreased water content of the cells and in part to closure of stomates. The guard cells are among the first cells to lose their turgidity when water deficits develop, resulting in closure of stomates. In at least some species closure of stomates greatly reduces entrance of carbon dioxide, thereby reducing photosynthesis. Water deficit also reduces the leaf area which further reduces the amount of tissue in which photosynthesis can occur. Reduction in photosynthesis tends to reduce growth by reducing the amount of food available. Unfortunately water deficit and wilting sometimes also increases the rate of respiration, thereby causing food to be used more rapidly at the same time that it is being synthesized more slowly.

The mineral nutrition of plants is also affected adversely by deficient soil moisture. Deficiency of boron often is more common in dry years and potassium is rendered less available by drying of the soil. The minerals in that portion of the soil which is dried to permanent wilting are unavailable because roots do not absorb from dry soil. In dry soil root growth ceases and the roots become suberized to the tips and relatively impermeable to both water and minerals. The activity of soil organisms is usually reduced, affecting the nitrogen supply. On the other hand the absorption of magnesium seems to be increased.

The chemical composition of plants often is materially affected by water deficit. Starch often disappears from wilting leaves. This is sometimes accompanied by an increase in sugar content, but not always. The nitrogen

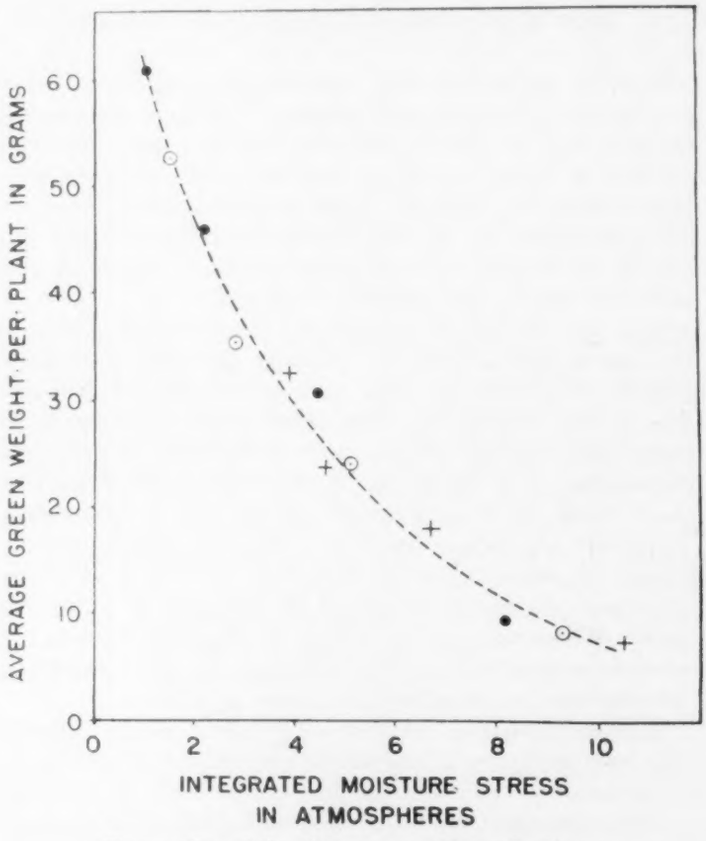

FIGURE 13.—*Soil moisture stress and growth of beans.*

metabolism is often disturbed, but the exact effects vary among different species. In some plants drought conditions result in the production of abnormal amounts of pentosan, hemicelluloses, and other compounds. Apparently in many instances moisture stress results in an unusually large proportion of the food being converted into cell wall materials, resulting in woody plant tissue which is low in nutritive value. Such occurrences are common, but very undesirable in pasture grasses and hay crops subjected to drought.

Not all the effects of moisture stress are undesirable. While vegetative growth is always reduced, the quality of fruits and seeds is sometimes improved by moderate moisture stress during ripening. Although yield of such fruit as apples, peaches, and pears is usually higher with heavy irrigation, the fruit is often softer and more easily bruised and sometimes inferior in taste to that ripened under moderate moisture stress. The quality of wheat also seems to be improved by occurrence of moisture stress during ripening. As shown in figure 10, moderate moisture stress decreases vegetative growth of guayule, but it greatly increases the rubber content. Plants "hardened" by exposure to moderate moisture stress for a short time before transplanting usually survive better than those kept heavily watered. It is evident that moisture supply should be adjusted according to the needs of the crop and nature of the season to obtain best results.

Effect of Field Capacity on Yield of Watersheds

The field capacity of a soil not only is important in respect to the availability of soil moisture for plant growth but also in terms of water storage capacity and water yield of watersheds. Movement of water in soil with a moisture content at or below field capacity is too slow to contribute to stream flow. If a soil is drier than field capacity, it must be wetted to field capacity before it will yield any water as runoff. The amount of water required to wet a soil to field capacity is much lower for sandy soils than for clays. For example, only 1.2 inches of water are required to wet 1 foot of Yolo fine sandy loam from the permanent wilting percentage to field capacity; but 3 inches are required to wet the Catherine loam up to the point where runoff begins. On a watershed with an average soil depth of 3 feet about 3.6 inches of rain would be required to wet dry Yolo fine sandy loam up to field capacity, where runoff would begin; but 9 inches would be required if the soil were Catherine loam or some other soil with equally high field capacity. Thus a foot of rainfall would yield 8.4 inches of runoff from the sandy loam but only 3 inches from a heavy loam or clay. Differences in soil texture therefore have important effects on water yield from watersheds.

Differences in soil structure also have important effects on runoff from a watershed because of the effect of soil structure on infiltration and temporary storage of gravitational water. Soils with a considerable proportion of large, noncapillary pores permit rapid infiltration and downward percolation of water. Such soils absorb water as rapidly as it falls, and runoff occurs chiefly through the soil rather than over the surface, hence erosion is negligible. Compact soils with few large pores permit very slow infiltration, resulting in heavy surface runoff and erosion. Watersheds of this type shed rain like a roof, often resulting in flash floods following severe rains. One of the chief benefits of well-managed forest cover on watersheds is its role in maintaining soil conditions favorable to rapid infiltration and maximum temporary storage (detention storage) of gravitational water, thereby slowing down runoff and reducing erosions and flood peaks. Overgrazing, in contrast, results in deterioration of soil structure, decreased infiltration, and increased erosion and flood damage.

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